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Marine birds and mammals of the Pacific Subarctic Gyres

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Abstract

The importance of the subarctic gyres of the North Pacific Ocean to marine birds and mammals is poorly known because of a paucity of data spanning appropriate scales of time and space. The little information that is available indicates the western subarctic gyre (WSAG) is more productive than the eastern subarctic gyre (ESAG). In summer the WSAG supports a greater density and higher biomass of seabirds than the ESAG, including at least two species that are more abundant at nesting colonies in the eastern subarctic. Perhaps most revealing of the seabird distributions in this regard is that of southern hemisphere shearwaters (*Puffinus* spp.) that overwinter in the North Pacific. Their biomass is an order of magnitude greater than that of any northern hemisphere species and is three-fold greater in the WSAG than in the ESAG. Several species of cetaceans also appear to be, or to have been prior to commercial depletions, more abundant in the WSA. Among the many prey species consumed by marine birds and mammals, squids and fishes in the family Myctophidae predominate overall. Other forage species, notably euphausiids, Pacific saury (*Cololabis saira*) and Atka mackerel (*Pleurogrammus monopterygius*) are important at times to certain species. The principal exceptions to this generalization are baleen whales and small seabirds that consume zooplankton. Interannual and decadal-scale variability in the physical environment and food web production affect seabirds and marine mammals at sea and at coastal breeding locations around the margins of the gyres.

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Contents

1. Introduction

Subarctic gyres are prominent oceanographic features of the North Pacific Ocean (Fig. 1). The Eastern Subarctic Gyre (ESAG) is formed by the North Pacific Current on the southern boundary and by the Alaska Current, the northern branch of the North Pacific Current, which forms the eastward and poleward boundaries of the gyre. The Alaska Current is broad (in the order of 300 km) on the eastern side of the Gulf of Alaska, but narrows to about 100 km in the western Gulf of Alaska and is the only significant current contributing to the flow around the ESAG (Reed & Schumacher, 1986). The comparatively narrow, high-speed, westward extension of the Alaska Current is commonly referred to as the Alaska Stream.

In contrast, circulation in and around the Western Subarctic Gyre (WSAG) is much more complex, with contributions from three major current systems that originate in distinct oceanographic settings (Favorite, Dodimead & Nasu, 1976). The Alaska Stream forms the northern boundary; the East Kamchatka Current, which originates in the Bering Sea, forms the western boundary; and the North Pacific Current forms the southern boundary. Varying amounts of each, as well as filaments of warm and cold-core rings formed in the mixing zone of the Kuroshio and Oyashio currents enter the gyre from around the perimeter.

The gyres provide linkage and exchange between subtropical and transitional waters of the North Pacific Ocean and arctic waters of the Bering Sea and Sea of Okh-

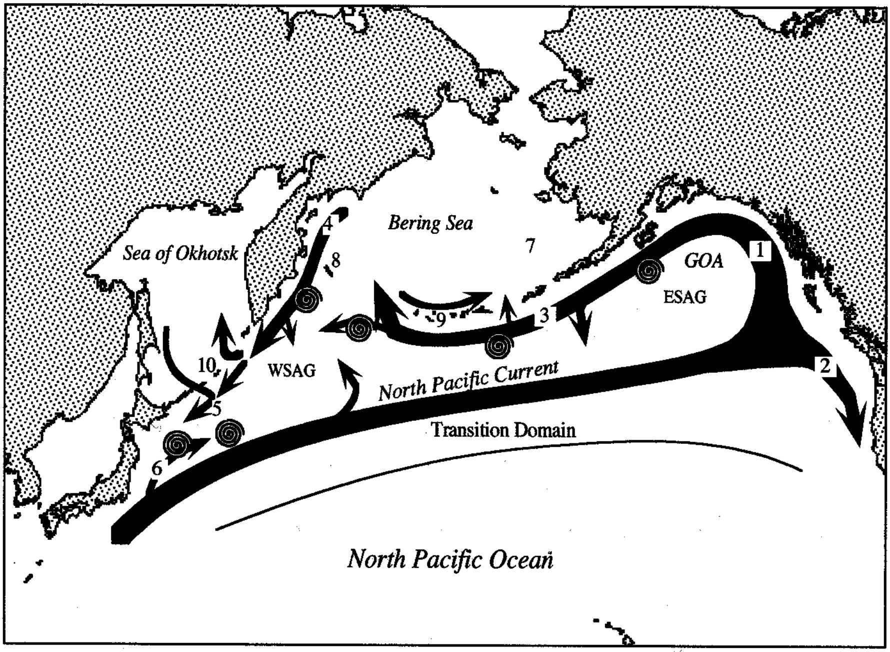

Fig. 1. Principal oceanographic features of the North Pacific Ocean and locations of the subarctic gyres. Based on data in Favorite et al. (1976). GOA—Gulf of Alaska; ESAG—Eastern Subarctic Gyre; WSAG—Western Subarctic Gyre; 1—Alaska Current; 2—California Current; 3—Alaska Stream; 4—East Kamchatka Current; 5—Oyashio Current; 6—Kuroshio Current extension; 7—Pribilof Islands; 8—Commander Islands; 9—Aleutian Islands; 10—Kurile Islands.

otsk. Consequently, the fauna is comprised of animals from all three domains, some resident, some migrating north, some south. Although coastal and shelf production is much higher during summer, the pelagic areas encompassed by gyres form an important wintering and nursery area for many species of birds and mammals that breed on shore around the perimeters.

Despite their physical prominence, little work has been done in the gyre areas with respect to birds and mammals owing to logistics and the distance from fishing zones or oil development areas on the continental shelf; the economic interests have given rise to many of the pelagic bird and mammal studies. Nonetheless, the gross distribution of seabirds and certain marine mammals have been, or can be, described and these will be reviewed here. Most previous analyses of the subarctic Pacific have focused on north-south variability and on species abundances and transitions from subarctic to subtropical waters, with emphasis on the boundaries (fronts). In contrast, we will focus more on the gyres themselves, describing when possible east-west similarities and differences in the composition, abundance, and biology of seabirds and marine mammals.

2. Sources of data

Published data used in this paper are referenced accordingly. Unpublished data on the pelagic distribution and abundance of marine birds were gathered during the 1970s and 1980s, largely under the Outer Continental Shelf Environmental Assessment Program (OCSEAP), and under the auspices of the U.S. Fish and Wildlife Service (USFWS). Included and analyzed here are all data archived under OCSEAP at the National Oceanographic Data Center (NODC) and by the USFWS (Anchorage, AK). A total of about 61 000 transects comprising 184 300 linear km of surveys were included for this analysis by Glenn Ford and Janet Casey (Ecological Consulting Inc., Portland OR) and John Piatt. These surveys are part of a database being prepared by the U.S. Geological Survey called *ACCESS*: A Computerized, Colony, Environment, and Seabirds-at-Sea database. Methods used to conduct transects and to analyze map distributions are summarized in Piatt and Ford (1993). Survey effort varied among seasons and PICES areas of interest. In particular, most transects were conducted in Summer (Jun–Aug, 49%) and Spring (Mar–May, 27%); far fewer were conducted in Autumn (Sep–Nov, 16%) or Winter (Dec–Feb, 7%). Survey effort was concentrated in Alaska continental shelf waters (Figs 2 and 3), and effort was limited in the eastern subarctic (ESA: 16 270 km) and western subarctic (WSA: 4380 km).

Unpublished data on seabirds nesting around the perimeter of the ESAG in Alaska came from the Seabird Colony Database of the USFWS. Unpublished data on cet-

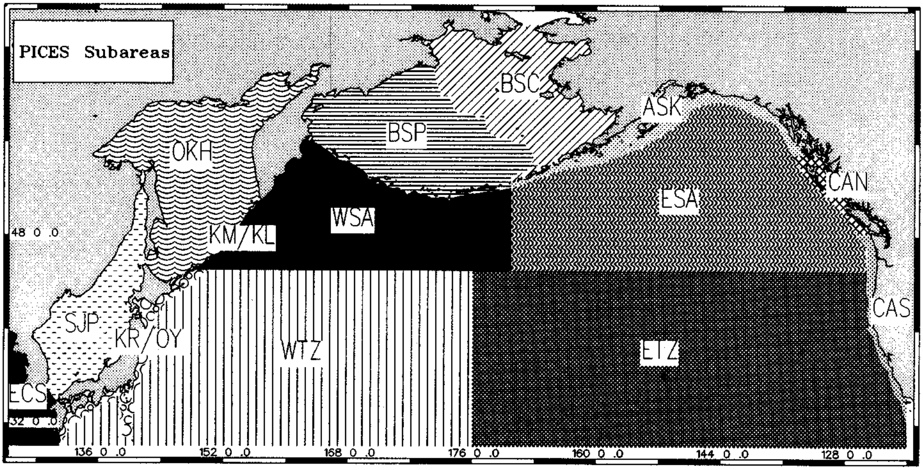

Fig. 2. PICES area (north of 30°N and including the marginal seas) and subareas of the North Pacific Ocean. BSC—Bering Sea Continental Shelf; BSP—Bering Sea Pelagic; ASK—Gulf of Alaska Continental Shelf; OKH—Sea of Okhotsk; KM/KL—Kurile Islands Region; WSA—Western Subarctic; ESA—Eastern Subarctic; CAN—Canadian Continental Shelf; SJP—Sea of Japan; KR/OY—Kuroshio/Oyahio Region; ECS—East China Sea; WTZ—Western Tropical Zone; ETZ—Eastern Tropical Zone; CAS—Canada Shelf. The ESA and WSA are deep water basins with boarders 200 m seaward of the continental shelf.

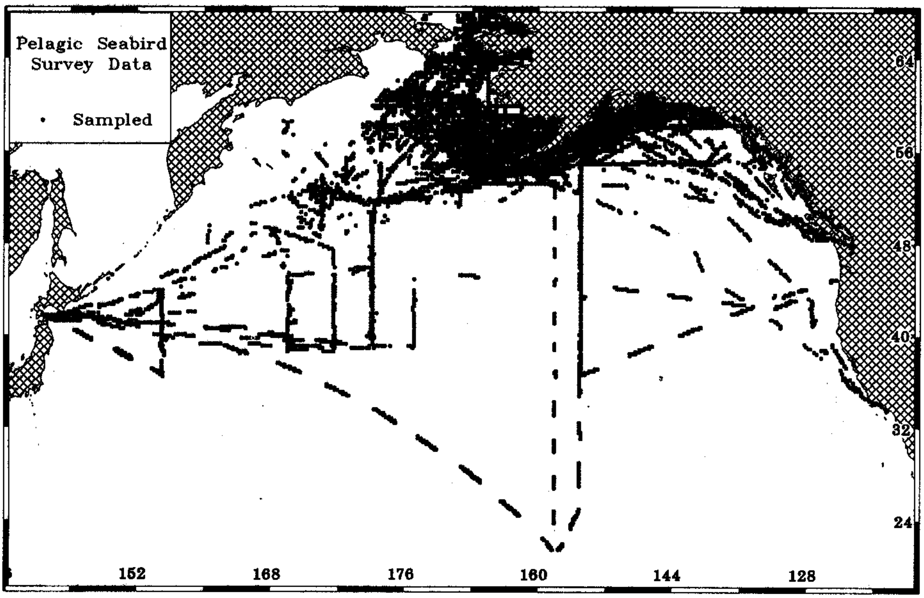

Fig. 3. Locations of transects censused for seabirds and included in the *ACCESS* data base.

aceans came from the International Whaling Commission, which has compiled harvest records from the North Pacific for the modern fishery that began in the late 1940s and lasted through the late 1970s.

3. Seabirds

3.1. Nesting abundance and distribution

The North Pacific Rim, including the Sea of Okhotsk and the Bering Sea, is home to some 90×10^6 nesting seabirds, of which 25×10^6 are found on the Asiatic side and 65×10^6 on the North American side (Shuntov, 1998). Abundances are similar around the perimeters of the WSA and ESA domains, in the order of 16×10^6 and 14×10^6, respectively (Table 1). These values undoubtedly would be higher if mammals had not been introduced to the Aleutian Islands and islands in the Gulf of Alaska beginning as early as 1750. Arctic foxes (*Alopex lagopus*), red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), and rodents (*Rattus norvegicus* and *Spermophilus undulatus*) were intentionally or accidentally released and devastated many species (Bailey & Kaiser, 1993; Litvinenko, 1993; Springer, Kondratyev, Ogi, Shibaev & Van Vliet, 1993).

Although numerous, individuals of the majority of species weigh less than 1 kg each, with many weighing < 0.1 kg, and so the estimated biomass of the nesting avifauna is only about 5600 t around the WSA and 5900 t around the ESA (Table

Table 1
Estimated abundances (in 1000s) of nesting seabirds in regions of the N. Pacific

English name	Scientific name	Kurile Is.[a]	E. Kamchatka[a]	Commander Is.[a]	Aleutian Is.[b]	Gulf of Alaska[b]	British Columbia[c]	Washington[d]	Abundance WSA[e]	Abundance ESA[f]	Biomass WSA[g]	Biomass ESA[g]
Northern fulmar	*Fulmarus glacialis*	1500	?	644	510	440	–	–	2654	440	1619	268
Fork-tailed storm-petrel	*Oceanodroma furcata*	200	–	20	2354	640	327	3.9	2574	971	129	49
Leach's storm-petrel	*Oceanodroma leucorhoa*	350	–	10	2483	1067	1039	36	2843	2142	142	107
Unidentified storm-petrel	*Oceanodroma* spp.						150	–	–	150	–	7.5
Double-crested cormorant	*Phalacrocorax auritus*	–	–	–	1.2	3.3	4.1	3.3	1.2	11	2.3	21
Brandt's cormorant	*Phalacrocorax penicillatus*	–	–	–	–	0.086	0.19	0.55	–	0.83	–	1.6
Pelagic cormorant	*Phalacrocorax pelagicus*	55	6.5	7	6	21	9	4.9	74.5	35	142	67
Red-faced cormorant	*Phalacrocorax urile*	25	10	2.2	26	20	–	–	63.2	20	120	38
Temminck's cormorant	*Phalacrocorax filamentosus*	7	–	–	–	–	–	–	7	–	13	–
Unidentified cormorant	*Phalacrocorax* spp.	–	–	–	9.1	15	–	–	9.1	15	17	29
Black-tailed gull	*Larus crassirostris*	1	–	–	–	–	–	–	1	–	0.75	–
Black-headed gull	*Larus rudibundus*	–	20		–	–	–	–	20	–	15	
Mew gull	*Larus canus*	+ ?	+	–	–	15	–	–	+	15	+	11
Ring-billed gull	*Larus delawarensis*	–	–	–	–	–	–	0.11	–	0.11	–	0.11
Herring gull	*Larus argentatus*	–	–	–	–	1	–	–	–	1	–	1
Slaty-backed gull	*Larus schistisagus*	< 90	35	–	–	–	–	–	125	–	163	–

Continued.

Table 1
Continued

English name	Scientific name	Kurile Is.[a]	E. Kamchatka[a]	Commander Is.[a]	Aleutian Is.[b]	Gulf of Alaska[b]	British Columbia[c]	Washington[d]	Abundance WSA[e]	Abundance ESA[f]	Biomass WSA[g]	Biomass ESA[g]
Glaucous-winged gull	*Larus glauscescens*	–	–	10	57	185	58	40	67	283	87	368
Black-legged kittiwake	*Rissa tridactyla*	< 90	6.2	54	60	675	–	–	210	675	84	270
Red-legged kittiwake	*Rissa brevirostris*	–	–	34	13	–	–	–	47	–	19	
Arctic tern	*Sterna paradisaea*	–	–	–	0.28	8.9	–	–	0.28	8.9	0.036	1.2
Aleutian tern	*Sterna aleutica*	–	–	–	0.41	9.4	–	–	0.41	9.4	0.053	1.2
Caspian tern	*Sterna caspia*	–	–	–	–	–	–	7.9	–	7.9	–	2.0
Common tern	*Sterna hirundo*	–	+	–	–	–	–	–	+	–	+	–
Unidentified tern	*Sterna* spp.	–	–	–	0.05	1.7	–	–	0.05	1.7	0.0065	0.22
Common murre	*Uria aalge*	300	10	60	43	589	8.6	31	413	629	413	629
Thick-billed murre	*Uria lomvia*	43	19	190	109	55	0.014	–	361	55	361	55
Unidentified murre[h]	*Uria* spp.	–	–	–	66	1197	–	–	66	1197	66	1197
Pigeon guillemot	*Cepphus columba*	> 5	1.1	3.2	15	24	9.3	4.3	24	38	13	20
Bridled guillemot	*Cepphus carbo*	< 5	–	–	–	–	–	–	5	–	2.7	–
Marbled murrelet	*Brac hyramphus marmoratus*	+	+	–	?	200	+	2.4	+	200	+	48.00
Kittlitz's murrelet	*Brachyramphus brevirostris*	–	+	–	?	+	–	–	+	+	+	+
Ancient murrelet	*Synthliboramphus antiquum*	3	13	0.1?	54	164	543	–	70	707	16	163
Cassin's auklet	*Ptychoramphus aleuticus*	–	–	–	118	355	2710	88	118	3153	24	631
Parakeet auklet	*Cerorhinca monocerata*	> 10	–	–	86	58	–	61	96	119	29	36

Continued.

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Continued

English name	Scientific name	Kurile Is.[a]	E. Kamchatka[a]	Commander Is.[a]	Aleutian Is.[b]	Gulf of Alaska[b]	British Columbia[c]	Washington[d]	Abundance WSA[e]	Abundance ESA[f]	Biomass WSA[g]	Biomass ESA[g]
Least auklet	*Aethia pusilla*	1	–	0.1	2278	0.02	–	–	2279	0.02	205	0.0018
Whiskered auklet	*Aethia pygmaea*	50?	–	5	6.5	–	–	–	62	–	9.3	–
Crested auklet	*Aethia cristatella*	1000	–	–	873	46	–	–	1873	46	562	14
Rhinoceros auklet	*Cyclorrhynchus psittacula*	< 1	–	10	0.03	170	719	–	11	889	5.8	471
Tufted puffin	*Lunda cirrhata*	175	18	200	1267	1093	78	23	1660	1194	1328	955
Horned puffin	*Fratercula corniculata*	3.5	0.4	5	91	773	0.053	–	100	773	55	425
TOTAL		3915	139	1255	10527	7826	5655	306	15835	13787	5642	5885

[a]From Velizhanin (1972); Velizhanin, (1978); Vyatkin (1986); Artyukhin (1991); Litvenenko and Shibaev (1991); Shuntov (1998).
[b]From U.S. Fish and Wildlife Service, seabird colony database: marbled murrelet in Gulf of Alaska from Piatt and Ford (1993).
[c]From Rodway (1991).
[d]From Speich & Wahl (1989).
[e]Kurile Is. + E. Kamchatka + Commander Is. + Aleutian Is.
[f]Gulf of Alaska + British Columbia + Washington.
[g]In tonnes; based on weights of seabirds presented by DeGange and Sanger (1986).
[h]Essentially all common murres.

1). Given the inherent difficulty in obtaining accurate estimates of numbers of many species, these values, like those of abundance, can be considered essentially the same.

Still, there are conspicuous differences in the west-east distribution of various species. Amongst the very abundant species, those that total $\geq 1 \times 10^6$, northern fulmars (*Fulmarus glacialis*), fork-tailed storm-petrels (*Oceanodroma furcata*), least auklets (*Aethia pusilla*), and crested auklets (*A. cristatella*) are much more numerous around the WSA, while common murres (*Uria aalge*), ancient murrelets (*Synthliboramphus antiquum*), Cassin's auklets (*Ptychoramphus aleuticua*), rhinoceros auklets (*Cyclorrhynchus psittacula*), and horned puffins (*Fratercula corniculata*) are much more numerous around the ESA. These differences likely reflect in part the trophic positions of the species and the nature of their foraging habitats and prey species available to them near the nesting sites. Nesting fulmars and storm-petrels typically forage over the shelf edge and deep water, fulmars feed on various fishes, squids, and medusae and the storm-petrels feed on small fishes, particularly juvenile lanternfishes (Myctophidae), squids, and euphausiids (DeGange & Sanger, 1986). Crested and least auklets feed primarily in oceanic waters where they can find concentrations of calanoid copepods, particularly *Neocalanus cristatus* and *N. plumchrus*, and euphausiids (Springer & Roseneau, 1985). Thus, all of these seabirds require ready access to oceanic habitats that are typical of the WSA, which has a very narrow or no continental shelf.

In contrast, the broader shelf of the ESA and the absence of islands near the shelf edge except in British Columbia preclude most of the planktivorous species. Black-legged kittiwakes (*Rissa tridactyla*), common murres, rhinoceros auklets, and horned puffins in the Gulf of Alaska feed mostly on the shelf on small forage fishes such as capelin (*Mallotus villosus*), sand lance (*Ammodytes hexapterus*), and juvenile walleye pollock (*Theragra chalcogramma*) (DeGange & Sanger, 1986; Hatch, 1984; Hatch & Sanger, 1992; Piatt & Anderson, 1996). In the Aleutian Islands, common murres are abundant only on those islands which have extensive shallow, shelf-like habitats surrounding them where they can find suitable prey (Springer, 1991; Springer, Piatt & Van Vliet, 1996a). Cassin's auklet is most abundant in British Columbia where it feeds at the shelf edge, primarily on *N. cristatus*, euphausiids, and small fish (Vermeer, 1984; Vermeer, Fulton & Sealy, 1985). Ancient murrelets, which are also most abundant in British Columbia, feed over the shelf and at the shelf edge on euphausiids and small forage fishes, particularly sand lance (Vermeer, 1984; Vermeer et al., 1985), which is most abundant in shallow continental shelf and shelf-like habitats.

Not all species of seabirds are favored in one region or the other, but appear to do equally well in both. Amongst the more evenly-distributed, abundant species are tufted puffins (*Lunda cirrhata*), which appear to be well-adapted to exploit a wide variety of prey (Hatch & Sanger, 1992), and Leach's storm-petrels (*Oceanodroma leucorhoa*), because they are truly pelagic birds able to exploit the extensive areas of pelagic habitat in both regions. Similarly, the less-abundant parakeet auklets (*Cerorhinca monocerata*) are relatively evenly distributed and also have catholic diets (Bedard, 1969; Harrison, 1990).

3.2. Pelagic abundance and distribution—general

In summer, most nesting seabirds are restricted to the vicinity of their breeding colonies and the nearby foraging areas. Nonbreeding adults and juveniles are more flexible and many remain at sea in the open North Pacific. Those birds are joined in summer by vast numbers of migrants from the southern hemisphere that spend the austral winter in the North Pacific. Among these, the sooty and short-tailed shearwaters (*Puffinus griseus* and *P. tenuirostris*) are most abundant, with an estimated population of 23×10^6 short-tailed shearwaters and apparently similar numbers of sooty shearwaters (Everett & Pitman, 1993). In winter, the shearwaters return south to nest whereas most of the resident North Pacific species disperse away from land into the ocean. Very little is known of the winter ecology of North Pacific seabirds, including specifics on wintering areas or diets.

At least 40 species of seabirds have been found at some time during the year in the subarctic North Pacific. Sanger and Ainley (1988) identified the 21 most common among them, as well as the ten dominant species (Table 2). They found that the most abundant species in summer were the shearwaters, with a combined contribution of over 50% of total numbers and over 60% of total biomass. The next most abundant species generally contributed at most 10% of numbers and biomass. The only excep-

Table 2
Most common species of seabirds and the 10 dominant species (number and/or biomass) at sea in the subarctic N. Pacific reported by Sanger and Ainley (1988)

English name	Scientific name	Dominant
Black-footed albatross	*Diomedea nigripes*	
Laysan albatross	*Diomedea immutabilis*	
Northern fulmar	*Fulmarus glacialis*	*
Sooty shearwater	*Puffinus griseus*	*
Short-tailed shearwater	*Puffinus tenuirostris*	*
Buller's shearwater	*Puffinus bulleri*	
Mottled petrel	*Pterodroma inexpectata*	
Streaked shearwater	*Calonectris leucomelas*	
Forked-tailed storm-petrel	*Oceanodroma furcata*	*
Leach's storm-petrel	*Oceanodroma leucorhoa*	*
Red phalarope	*Phalaropus fulicarius*	*
Herring gull	*Larus argentatus*	
Glaucous-winged gull	*Larus glauscescens*	*
Black-legged kittiwake	*Rissa tridactyla*	*
Arctic tern	*Sterna paradisaea*	
Thick-billed murre	*Uria lomvia*	*
Ancient murrelet	*Synthliboramphus antiquum*	
Cassin's auklet	*Ptychoramphus aleuticus*	
Rhinoceros auklet	*Cyclorrhynchus psittacula*	
Tufted puffin	*Lunda cirrhata*	*
Horned puffin	*Fratercula corniculata*	

tion was in the WSA, where Leach's storm-petrels (*Oceanodroma leucorhoa*) constituted nearly 20% of numbers, but less than 5% of biomass.

Counts of seabirds on a transect run along 155°W from Alaska to Hawaii indicated an affinity of some species for the gyre of the ESA in summer (Day, 1992). Overall seabird density was highest over the center of upwelling of the gyre in 1984 (24 birds km^{-2}) and at the southern edge in 1985 (28 birds km^{-2}) particularly because of the relatively high abundances of short-tailed and sooty shearwaters, as well as mottled petrels (*Pterodroma inexpectata*) and pomarine jaegers (*Stercorarius pomarinus*). However, the frequency of occurrence of seabirds sighted during count intervals and the species diversity were both comparatively low in the center of the gyre.

On a similar transect run along 158°W in fall 1976, Gould (1983) found the highest density, approximately 45 birds km^{-2} consisting mainly of short-tailed and sooty shearwaters, between 55–54°N. Density dropped to 8 birds km^{-2} between 53–52°N in the Subarctic Current and remained comparatively uniform until approximately 41°N, where it declined further to 1–2 birds km^{-2} at the southern edge of the Transition Domain. According to Gould, the region of highest densities for all birds occurred "...in the cold, nutrient-rich waters of the Alaska Current System near its border with the Ridge Domain." This is also the region of the continental shelf edge, which is known to be a highly productive habitat in the North Pacific (Parsons, 1986; Springer, McRoy & Flint, 1996b) and might have further contributed to its importance to seabirds.

In spite of the small areal coverage, comparisons of seabird abundances between regions of the subarctic North Pacific have been made (Table 3). Sanger and Ainley (1988) considered three geographic areas: Western Subarctic, Central Subarctic, and Gulf of Alaska. The Western and Central Subarctic are subsumed in the WSA and the Gulf of Alaska includes the bulk of the ESA. Both density and biomass of seabirds were similar in the western and eastern regions of the subarctic, about 12–15 birds km^{-2} (8–10 kg km^{-2}), and were somewhat lower in the central region, about 8 birds km^{-2} (5 kg km^{-2}).

Wahl, Ainley, Benedict and DeGange (1989) ambitiously subdivided the North Pacific into 20 subareas, including regions identified as the WSAG and ESAG. A somewhat greater contrast between east and west was apparent from this analysis (Table 3). Seabird abundance was estimated to be about 4 birds km^{-2} in the ESAG

Table 3
Comparisons of estimates of seabird density (birds km^{-2}) in regions of the subarctic N. Pacific. WSA—Western Subarctic; WSAG—Western Subarctic Gyre; ESA—Eastern Subarctic; ESAG—Eastern Subarctic Gyre

Source	WSA	WSAG	ESA	ESAG	E:W
Sanger and Ainley (1988)	12		15		1:0.8
Wahl et al. (1989)		23		4	1:5.8
ACCESS	24		8		1:3.3

and about 23 birds km^{-2} in the WSAG, a ratio of 1:5.8. Seabird biomass was estimated to be 2 kg km^{-2} in the ESAG and 9 kg km^{-2} in the WSAG, a ratio of 1:4.5.

Our analysis of data in *ACCESS* indicated overall abundances in summer of about 8 birds km^{-2} in the ESA and 24 birds km^{-2} in the WSA (Table 3), a ratio of 1:3. An even greater east-west difference exists to the south between the eastern subtropical zone and the western subtropical zone, where the ratio of densities is about 1:24 (Fig. 4). In terms of total numbers, in the order of 29 million seabirds can be found at sea in the ESA in summer compared to 51 million in the WSA, a ratio of just 1:1.8, because of the larger surface area of the region defined as the ESA.

These differences in numerical abundances in summer between west and east contrast with the more even abundance of nesting birds in the two regions (Fig. 5). Differences between the estimates may be attributed largely to the pelagic surveys also including non-breeders and migrants.

Abundances of the most common species or taxa computed from *ACCESS* data are shown in Table 4. The combined density and biomass of short-tailed and sooty shearwaters (*Puffinus* spp.) are nearly an order of magnitude greater than the next most abundant species or taxon in both the WSA and ESA, and are 3-fold more abundant in the WSA than in the ESA. However, Gould (pers. comm.) has recalculated *ACCESS* data and suggests that the biomass of Laysan albatrosses in the WSA is equal to or higher than that of sooty shearwaters and that the biomass of short-tailed shearwaters in both the WSA and ESA is much less than the biomass of sooty shearwaters.

Other species also show distinct east-west differences in abundance, which in several cases reflect differences in nesting distributions. For example, the fulmar, storm-petrels, *Aethia* auklets, and tufted puffins are all more abundant both as nesting species and at sea in the WSA. In contrast, black-legged kittiwakes and horned puf-

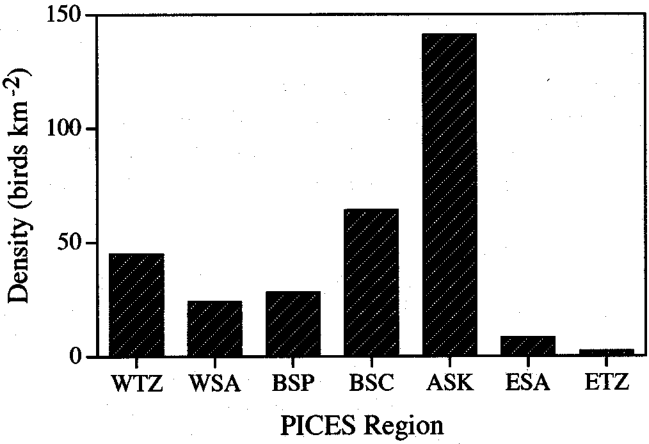

Fig. 4. Densities of seabirds in the North Pacific in summer. Data from *ACCESS*. WTZ—Western Tropical Zone; WSA—Western Subarctic; BSP—Bering Sea Pelagic; BSC—Bering Sea Continental Shelf; ASK—Gulf of Alaska Continental Shelf; ESA—Eastern Subarctic; ETZ—Eastern Tropical Zone.

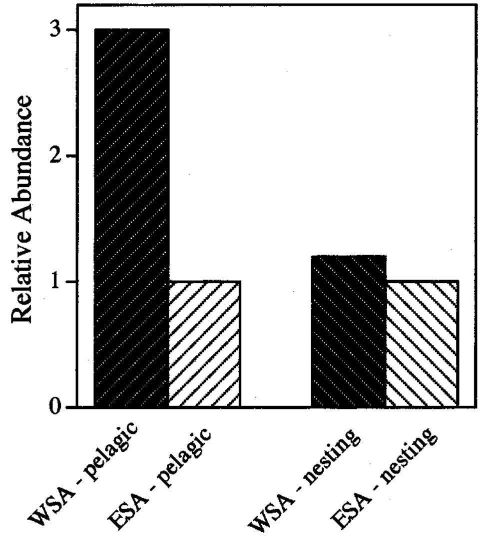

Fig. 5. Comparisons of abundances of seabirds nesting and at-sea in the western and eastern subarctic North Pacific. Data for nesting abundance from Table 1; data for at-sea abundance from *ACCESS*; WSA—Western Subarctic, ESA—Eastern Subarctic.

fins are more abundant as nesting species in the ESA but more abundant at sea in the WSA.

These estimates of the summer abundances of seabirds in the WSA are substantially higher than estimates based on data from the region compiled by VPS (pers. comm.). Those data indicate that in most years seabird densities are only about 10 birds km^{-2} on the shelf and slope within a few 10s of miles off the coast, and decline to about 5 birds km^{-2} in the open ocean less than 200 miles offshore and to 1–2 birds km^{-2} up to 300 miles offshore. At present this discrepancy can not be reconciled, but is possibly related to differences in survey techniques.

Many of the birds counted at sea in summer are non-breeding individuals, being either immature northern hemisphere species or southern hemisphere species (both immature and adults). Specimens recovered from the squid drift net fishery in the 1980s consisted predominantly of immatures, e.g., 79% and 88% of all sooty and short-tailed shearwaters, respectively, indicating that this region is an important nursery area for these two species (Gould & Piatt, 1993).

There are notable seasonal differences in abundances of pelagic seabirds in the ESA: highest bird densities (29 birds km^{-2}) occur in spring, declining to 8 birds km^{-2} in summer, to 3 km^{-2} in fall, and < 1 bird km^{-2} in winter (*ACCESS*). The high spring densities are likely related to migrations by shearwaters through the region.

Too few counts exist in the *ACCESS* data set to allow estimates of abundance in the WSA for seasons other than summer. Shuntov (1972) estimated that offshore, densities of seabirds in the WSA in winter were only 0.4 birds km^{-2}, about the same as in the ESA. More recent data from later in the winter suggest somewhat higher densities of 0.8–2.2 birds km^{-2} occur offshore. The most important winter-time con-

Table 4
Abundance of the most common seabirds at sea in summer (Jun–Aug) in the western and eastern subarctic N. Pacific (WSA & ESA)[a]

English name	Scientific name	Density (birds km^{-2})		Biomass (grams km^{-2})	
		WSA	ESA	WSA	ESA
Black-footed albatross	*Diomedea nigripes*	0.040	0.10	124	310
Laysan albatross	*Diomedea immutabilis*	0.71	0.0078	1740	19
Northern fulmar	*Fulmarus glacialis*	1.5	0.72	915	439
Shearwaters	*Puffinus spp.*	16	4.7	12 000	3525
Buller's shearwater	*Puffinus bulleri*	0.0013	0.0018	1.0	1.4
Gadfly petrels	*Pterodroma spp.*	0.78	0.28	273	98
Fork-tailed storm-petrel	*Oceanodroma furcata*	1.5	0.44	90	26
Leach's storm-petrel	*Oceanodroma leucorhoa*	1.4	0.49	70	25
Other storm-petrels	*Oceanodroma spp.*	0.37	0.21	20	12
Red phalarope	*Phalaropus fulicarius*	0.040	0.00059	1.6	0.02
Gull	*Larus spp.*	0.045	0.066	52	76
Black-legged kittiwake	*Rissa tridactyla*	0.28	0.12	112	48
Murres	*Uria spp.*	0.022	0.0042	22	4.2
Least auklet	*Aethia pusilla*	0.022	0	2.2	0
Crested auklet	*Aethia cristatella*	0.18	0	54	0
Tufted puffin	*Lunda cirrhata*	0.41	0.07	326	56
Horned puffin	*Fratercula corniculata*	0.039	0.0038	21	2.1
TOTAL		23	7.2	15 824	4641

[a]Density data from *ACCESS*; biomass calculated from weights in DeGange and Sanger (1986).

centrations of seabirds in the WSA occur near the Kurile Islands and off the southeastern part of the Kamchatka Peninsula, where densities reached 10–12 birds km^{-2} earlier in winter. Data from later in the winter suggest lower densities on the shelf and slope of 4–9 birds km^{-2}.

In addition to the contrasts in the overall densities of seabirds between ESA and WSA, the *ACCESS* data reveal interregional differences in the proportions of different feeding types. In summer, shearwaters, which have a variety of foraging behaviors (surface seizing, plunging, and diving to moderate depths) contribute the greatest number and biomass in both regions, and the ratio of abundance of shearwaters in the ESA and WSA was 1:3.4, similar to the overall ratio of abundances (1:3). However, the ESA:WSA ratio for murres, which forage by diving to depths of up to 200 m, was about 1:5.2. Wahl et al. (1989) reported similar differences between the ESAG and the WSAG; surface feeders constituted about 60% to 70% of total numbers in the ESAG, but < 50% in the WSAG. In terms of biomass, the contrast was even more striking. Surface feeders constituted about half the biomass of seabirds in the ESAG, but only about 10% in the WSAG. Thus, the seabird fauna of the ESA has proportionally more seabirds that forage at or near the surface of the ocean, while the WSA has relatively more seabirds that forage at greater depths.

3.3. Pelagic abundance and distribution—specific

At present, the *ACCESS* database is being updated and refined so here we have analyzed species distributions only with regard to major PICES areas. However, earlier distributional maps prepared by Shuntov (1972) give some perspective on distributions of selected species in relation to the subarctic North Pacific.

In summer the Laysan albatross (*Diomedea immutabilis*) is abundant in the WSA, including most of the area occupied by the gyre (Fig. 6). The black-footed albatross (*Diomedea nigripes*) replaces the Laysan albatross in the ESA, but it is noticeably less abundant across the center of the gyre (Fig. 7). In winter, Laysan albatrosses remain in the WSA, but apparently are less abundant toward the center of the gyre than in summer. The black-footed albatross, in contrast, moves south out of the subarctic in winter. *ACCESS* data support the view of a skewed distribution of these species (Table 4).

Fulmars are widely distributed across the subarctic North Pacific throughout the year, but are generally more abundant in the center of the WSA than the center of the ESA, where they occur primarily around the northern margin (Fig. 8). *ACCESS* data also indicate that fulmars are more abundant around the perimeter, particularly near the shelf edge.

3.4. Diets

Summertime diets of most species of seabirds at the nesting colonies are comparatively well-known. The planktivorous species rely primarily on large calanoid copepods and euphausiids, whereas the most highly piscivorous species, the common murre, depends on various forage fishes, particularly sand lance (DeGange & Sanger, 1986; Springer, 1991). Thick-billed murres (*Uria lomvia*) nesting in the western Aleutian Islands feed primarily on squids (Springer et al., 1996a). Nesting tufted puffins and horned puffins in both the ESA and WSA feed on squids as well as a variety of species of forage fishes (Hatch & Sanger, 1992; Springer et al., 1996a; Wehle, 1976). Fulmars feed primarily on squids, forage fishes, and jellyfish (Hatch, 1993), and storm-petrels feed on squids, euphausiids, other crustaceans, and small forage fishes, particularly myctophids (Vermeer & Devito, 1988; Watanuki, 1985).

Comparatively little information is available for the diets of most species when they are away from the nesting colonies at sea. The main exceptions are short-tailed and sooty shearwaters, thick-billed murres, and tufted puffins in the WSA in spring and summer (Ogi, 1980, 1984; Ogi, Kubodera & Nakamura, 1980) whose diets were analysed from birds entangled in salmon gill nets during the 1970s in several areas of the western North Pacific (Fig. 9). Comparable offshore data for the ESA are lacking.

Springtime diets of thick-billed murres varied depending on location in the WSA (Fig. 10). Juvenile Atka mackerel (*Pleurogrammus monopterygius*) of 20–35 mm in length were the primary prey of birds in Okhotsk Water at the southern end of the Kurile Islands in the extreme southwestern region of the WSA. Whereas at the northern end of the Kuriles, in the East Kamchatka Current, their diets were dominated by euphausiids, primarily *Thysanoessa inermis*, and fish (mostly juvenile Atka mackerel) were of relatively little importance.

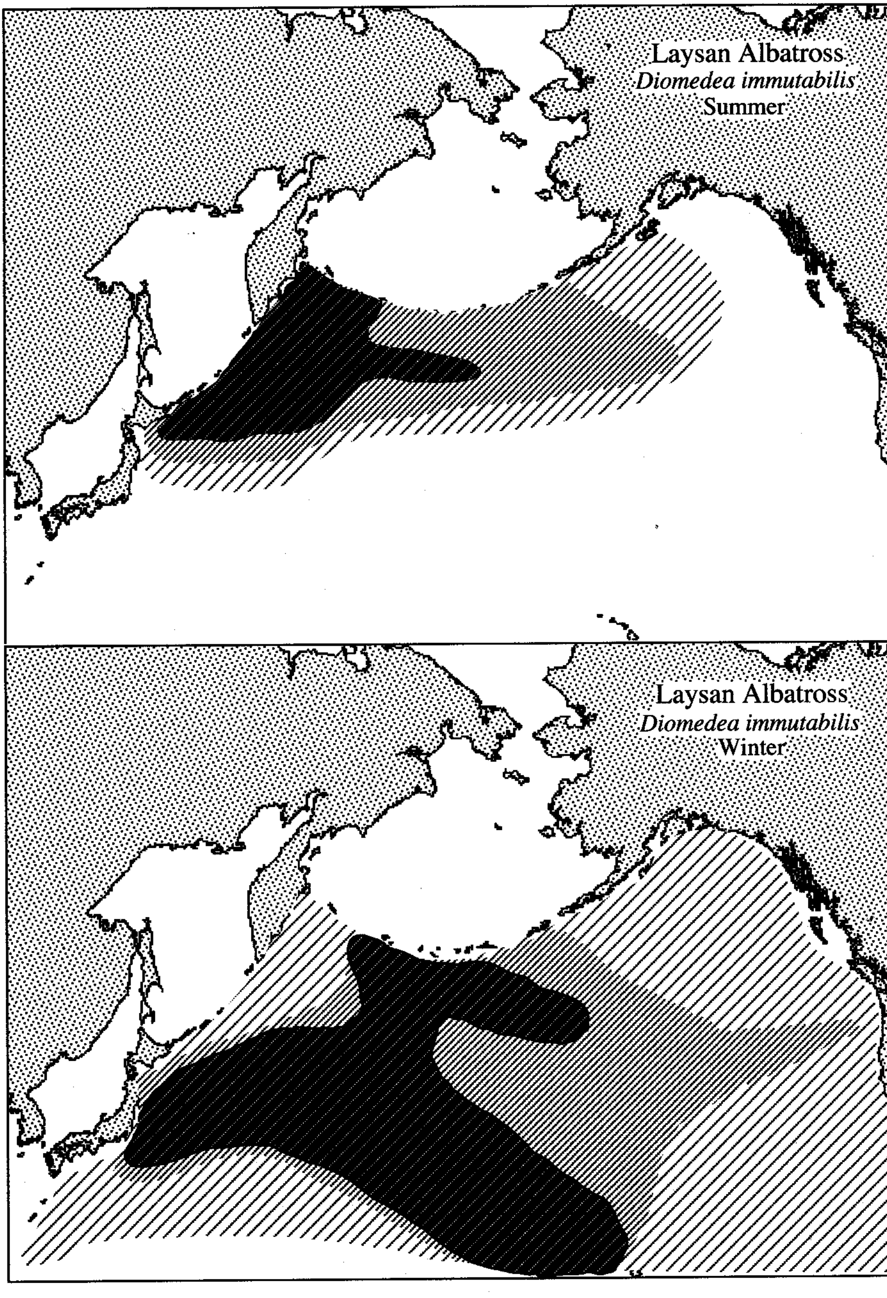

Fig. 6. Generalized distribution of Laysan albatrosses in the subarctic North Pacific. Redrawn from Shuntov (1972).

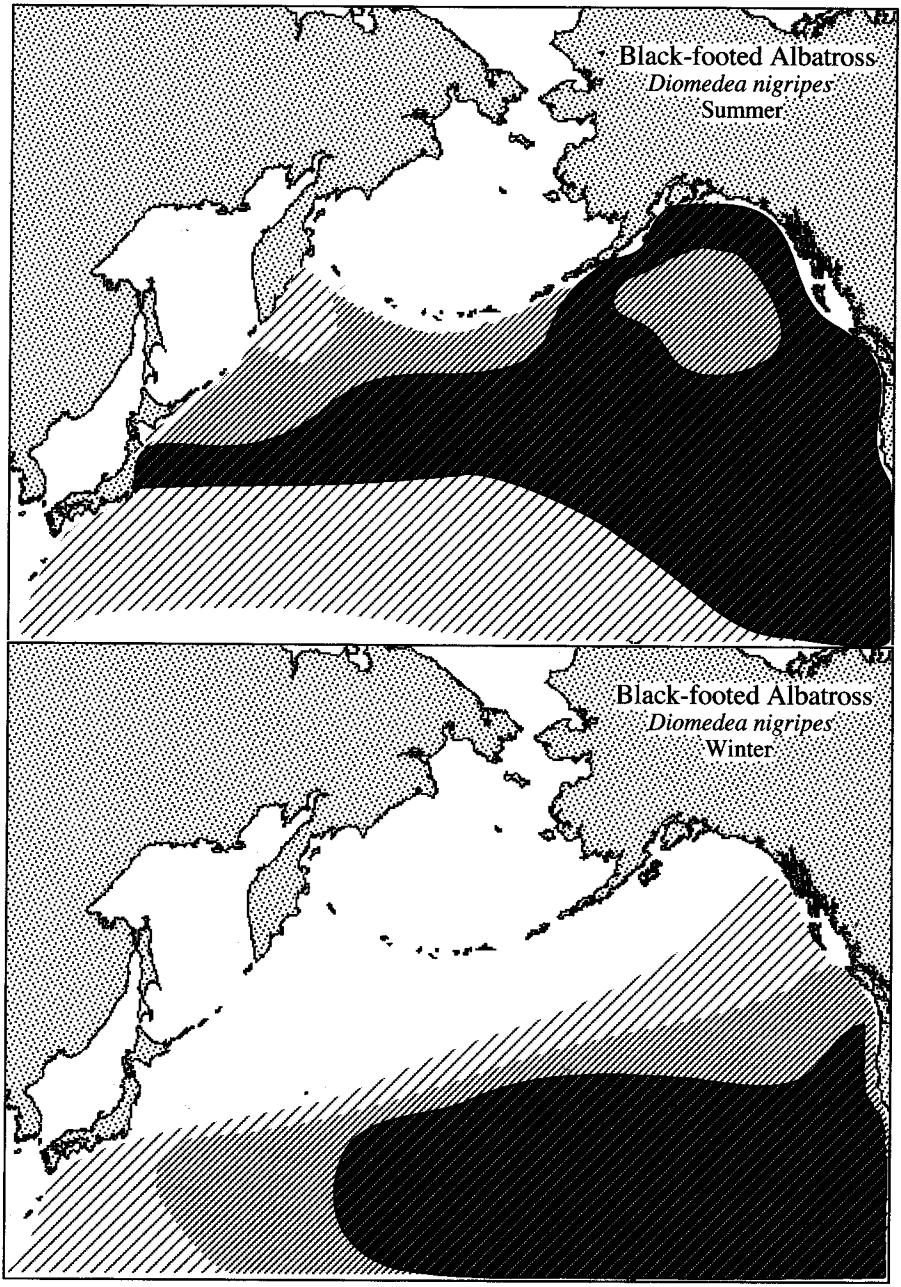

Fig. 7. Generalized distribution of black-footed albatrosses in the subarctic North Pacific. Redrawn from Shuntov (1972).

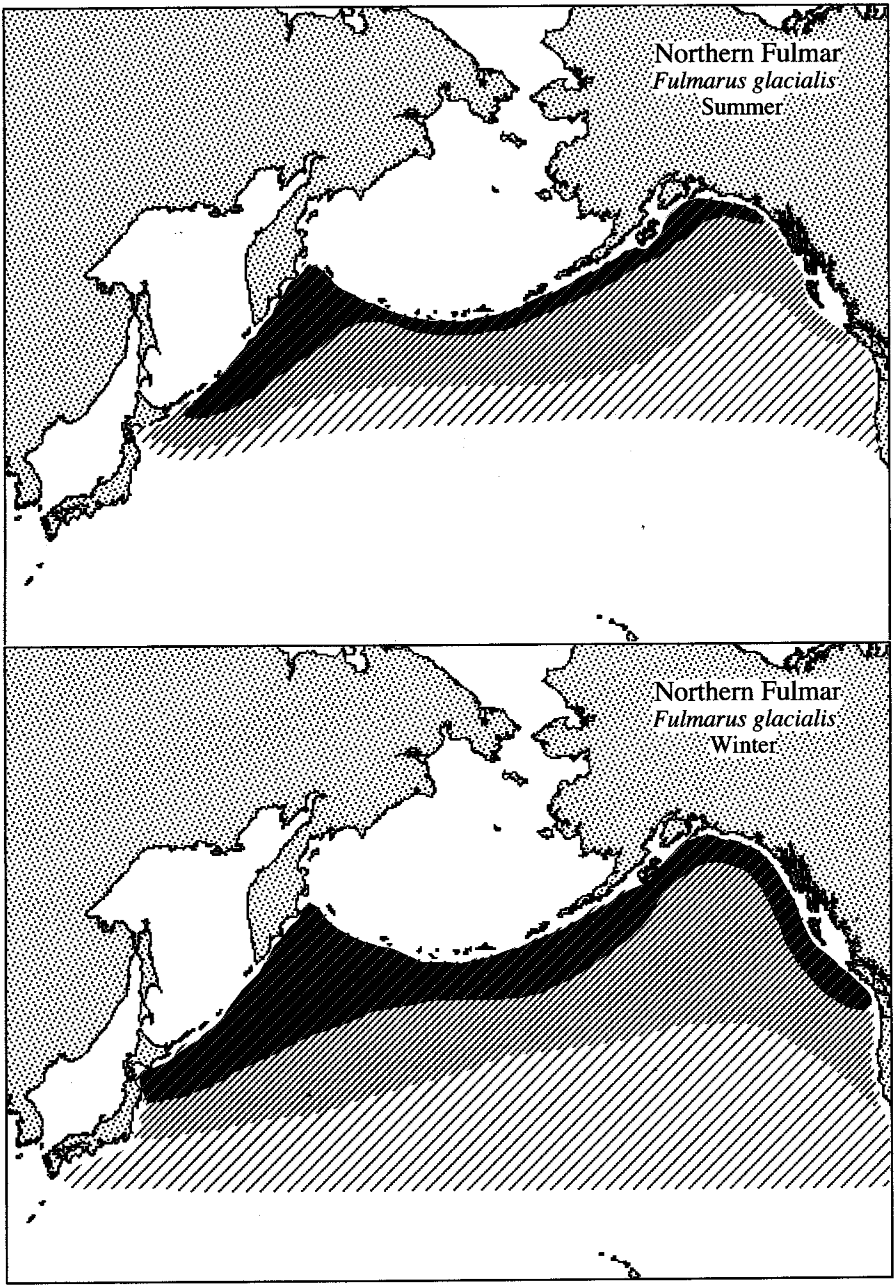

Fig. 8. Generalized distribution of northern fulmars in the subarctic North Pacific. Redrawn from Shuntov (1972).

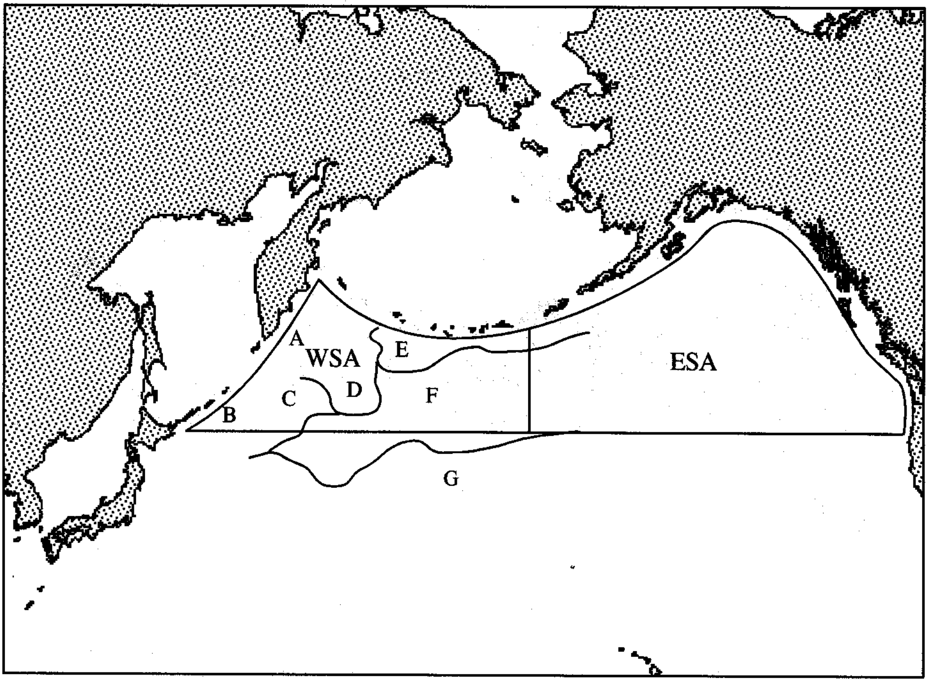

Fig. 9. Regions of the North Pacific identified by Ogi (1980) and Ogi et al. (1980) and the locations of PICES regions Western Subarctic (WSA) and Eastern Subarctic (ESA). A—East Kamchatka Current; B—Okhotsk Water; C. Subarctic Current 1; D. Western Subarctic Gyre; E. Alaskan Stream; F. Subarctic Current 2; G—West Wind Drift.

Elsewhere in the WSA, diets of thick-billed murres consisted mainly of squids, mostly *Berryteuthis magister* but also including *B. anonychus* and *Gonatopsis borealis*. Fishes were abundant in diets at few stations, but were taken in small numbers at most stations. The major fish species were lanternfishes (*Stenobrachius nanochir*, *S. leucopsarus*, and *Tarletonbeania crenularis*) and three-spined sticklebacks (*Gasterosteus aculeatus*). Euphausiids (*Thysanoessa longipes*) were generally of little importance compared to squids or fish. Other taxa of prey were apparently not important in offshore areas.

The diets of tufted puffins were not well quantified, but differed in some respects from those of murres. For example, in Okhotsk Water in the southwestern region, the tufted puffins were feeding on fish, squid, and euphausiids. In the Subarctic Current, the fishes being consumed by tufted puffins were Atka mackerel and northern smoothtongue (*Leuroglossus stilbius*), whereas thick-billed murres took mostly lanternfish and sticklebacks.

Diets of short-tailed shearwaters in spring also varied by region in the WSA (Fig. 11). Fish were the most important items everywhere except the Western Subarctic Current and West Wind Drift, where squid dominated. The fish species consumed were mostly juvenile *Pleurogrammus* spp. and small-sized lanternfishes

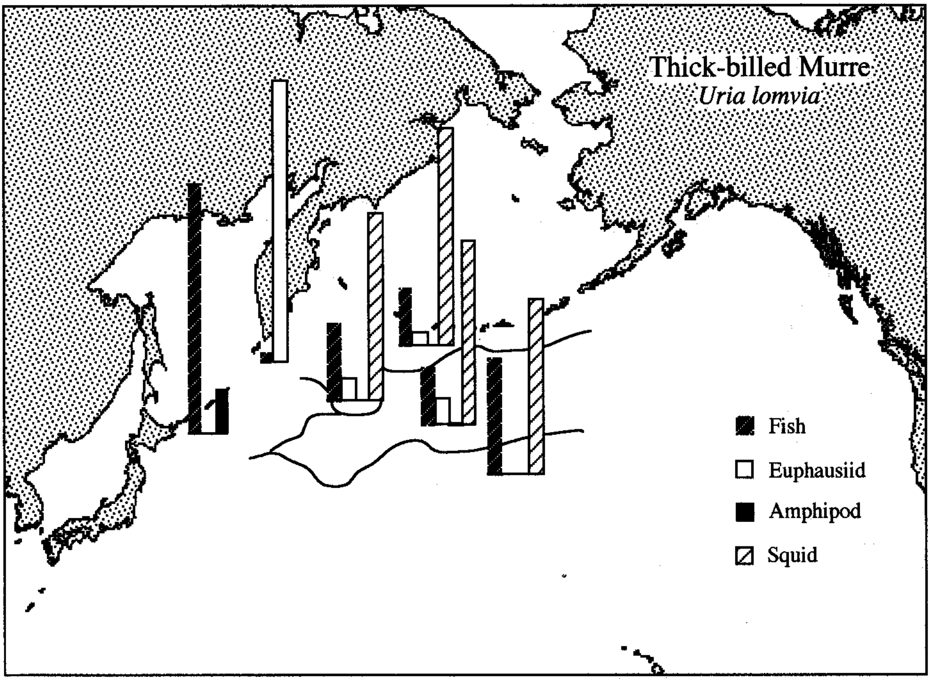

Fig. 10. Diets of thick-billed murres in the subarctic North Pacific. Values in % total weight of prey; data from Ogi (1980).

(Myctophidae). Diets were most diverse in the WSAG, where euphausiids ranked second by weight (19%) and third in number (23%); all the individuals identified were *Thysanoessa longipes*. Amphipods ranked second in frequency of occurrence (33%), but they were of minor importance on a weight basis. All but one of the individuals identified were either *Parathemisto japonica* or *P. pacifica*. Copepods, primarily *Neocalanus cristatus*, ranked fourth in weight (12%) and third in frequency of occurrence (30%). Squid ranked third in weight (14%) and fifth in frequency of occurrence (17%); the only individual identified was *Chiroteuthis* spp.

The diets of short-tailed shearwaters in WSA apparently reflect the availability of prey species rather than dietary preferences, since elsewhere, e.g., in the Sea of Okhotsk, Bering Sea, and West Wind Drift in summer, Ogi et al. (1980) found other prey to predominate. Over the shelf of the Sea of Okhotsk offshore of the southwestern Kamchatka Peninsula, euphausiids constituted about 85% of the diet, with fish being found in just one of 18 birds examined. In the Bering Sea, the diet consisted of 73% euphausiids, 14% squids, 8% amphipods, and just 5% fish. In the West Wind Drift, the only prey were squids and jellyfish. Thus, shearwaters will feed on a variety of species, selecting among them those that are most available within their foraging depth.

Fish, particularly Pacific saury (*Cololabis saira*), were important prey of sooty shearwaters throughout summer in the Subarctic Current and Transition Domain and

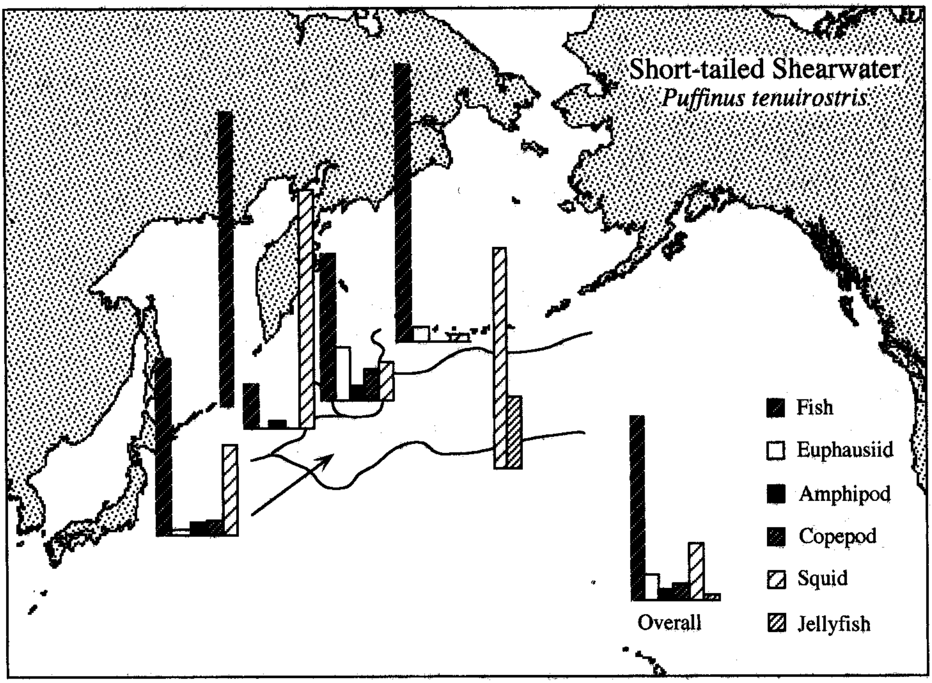

Fig. 11. Diets of short-tailed shearwaters in the subarctic North Pacific. Values in % total weight of prey; data from Ogi et al. (1980).

in late summer in the Alaska Stream (Fig. 12). The saury is a warm-water species that migrates north in summer as water temperature rises, ranging across the entire northwestern Pacific by August. Ogi (1984) believes that the movements of shearwaters coincide with the movements of the sauries. Squid were also important prey of sooty shearwaters, with increasing prominence at higher latitudes. They occurred in 100% of samples from the Alaska Stream and Subarctic Current, 67% of samples from the Transition Domain, and 41% of samples from the Subtropic region.

The importance of Pacific saury in the diets of other species of seabirds also increases south of the subarctic domains. Prey (as distinct from fish and squid scavanged from driftnets) of Bullers' shearwaters (*Puffinus bulleri*) killed in the high-seas driftnet fisheries in the Transition Domain (39°N to 46°N, 160°E to 150°W) were predominantly saury throughout summer (Gould, Ostrom & Walker, 1998). Prey of flesh-footed shearwaters (*Puffinus carneipes*) from approximately the same area, in summer to fall, likewise consisted primarily of saury, with a lesser amount of myctophids (Gould, Ostrom & Walker, 1997a). Laysan albatrosses from the Transition Domain in summer preyed primarily on saury, myctophids, and squids in the families Gonatidae and Cranchiidae, while black-footed albatrosses were preying primarily on squids with small amounts of fish or other invertebrates (Gould, Ostrom & Walker, 1997b).

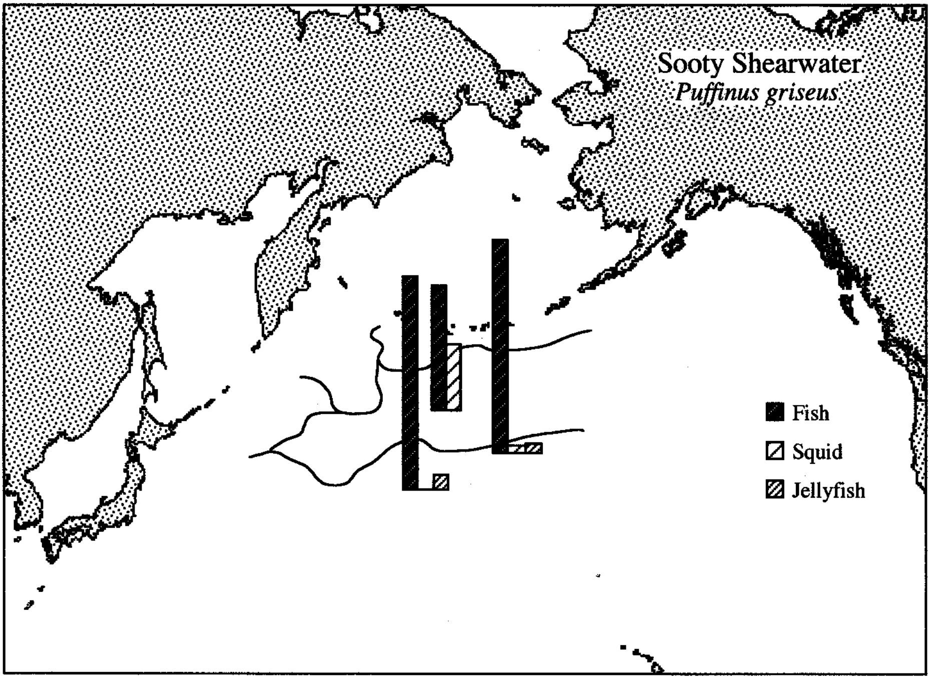

Fig. 12. Diets of sooty shearwaters in the subarctic North Pacific. Values in % total weight of prey; data from Ogi (1984).

4. Marine mammals

Twenty-four species of cetaceans are found in and around the subarctic North Pacific during the spring and summer seasons (Table 5). Seven species of pinnipeds have breeding populations around the margin of the North Pacific in the coastal zone, as do sea otters (*Enhydra lutra*). Of these, only the northern fur seal (*Callorhinus ursinus*) occurs in large numbers distant from land as it disperses from rookeries on the Kurile, Commander, and Pribilof islands. During summer fur seals mostly forage in waters close to the islands where their rookeries are located (Goebel, Bengtson, DeLong, Gentry & Loughlin, 1991). Steller sea lions (*Eumetopias jubatus*) are abundant around the perimeter of the subarctic North Pacific but only venture short distances into the open ocean to forage. All the other pinnipeds and the sea otter remain close to shore throughout the year, and are not considered to be part of the fauna of the subarctic gyres. One additional species, the northern elephant seal (*Mirounga angustirostris*) migrates to the ESA from breeding sites off southern California.

4.1. Cetaceans

Today, Dall's porpoises (*Phocoenoides dalli*) are likely to be the most abundant species of marine mammals in the ESA and WSA. Buckland, Cattanach and Hobbs

Table 5
Marine mammals of the subarctic North Pacific[a]

English name	Scientific name	Western Subarctic	Eastern Subarctic
Northern right whale	*Eubalaena glacialis*	x	x
Blue whale	*Balaenoptera musculus*	x	x
Fin whale	*Balaenoptera physalus*	x	x
Sei whale	*Balaenoptera borealis*	x	x
Bryde's whale	*Balaenoptera edeni*	x	
Minke whale	*Balaenoptera acutorostrata*	x	x
Humpback whale	*Megaptera novaeangliae*	x	x
Gray whale	*Eschrichtius robustus*	x	x
Sperm whale	*Physeter catodon*	x	x
Belukha whale	*Delphinapterus leucas*	x	x
Baird's beaked (Bottlenose) whale	*Berardius bairdii*	x	x
Cuvier's beaked (Goosebeak) whale	*Ziphius cavirostris*	x	x
Stejneger's beaked whale	*Mesoplodon stejnegeri*	x	x
Killer whale	*Orcinus orca*	x	x
Short-finned pilot whale	*Globicephala macrorhynchus*	x	x
False killer whale	*Pseudorca crassidens*	x	x
Pacific white-sided dolphin	*Lagenorhynchus obliquidens*	x	x
Risso's dolphin	*Grampus griseus*	x	x
Bottlenose dolphin	*Tursiops truncatus*	x	
Striped dolphin	*Stenella coeruleoalba*	x	
Common dolphin	*Delphinus delphis*	x	
Northern right whale dolphin	*Lissodelphis borealis*	x	x
Dall's porpoise	*Phocoenoides dalli*	x	x
Harbor porpoise	*Phocoena phocoena*	x	x
Steller sea lion	*Eumetopias jubatus*	x	x
California sea lion	*Zalophus californianus*		x
Northern fur seal	*Callorhinus ursinus*	x	x
Northern elephant seal	*Mirounga angustirostris*		x
Bearded seal	*Erignathus barbatus*	x	
Harbor seal	*Phoca vitulina*	x	x
Ribbon seal	*Phoca fasciata*	x	
Spotted (Largha) seal	*Phoca largha*	x	
Sea otter	*Enhydra lutris*	x	x
Number of species		31	26

[a]From Jefferson, Leatherwood and Webber (1993).

(1993) estimated the population in the North Pacific to be about 1.2×10^6 based on observations by U.S. observers on Japanese salmon research vessels and U.S. vessels, as well as on vessels engaged in the squid and albacore driftnet fisheries in the North Pacific. Dall's porpoises are widespread throughout most of the subarctic and appear to be equally abundant in ESA and WSA (Fig. 13). They show a distinct preference for subarctic waters, with a sharp decline in abundance across the subarctic frontal zone.

Diets of Dall's porpoises consist primarily of squid and numerous species of fishes,

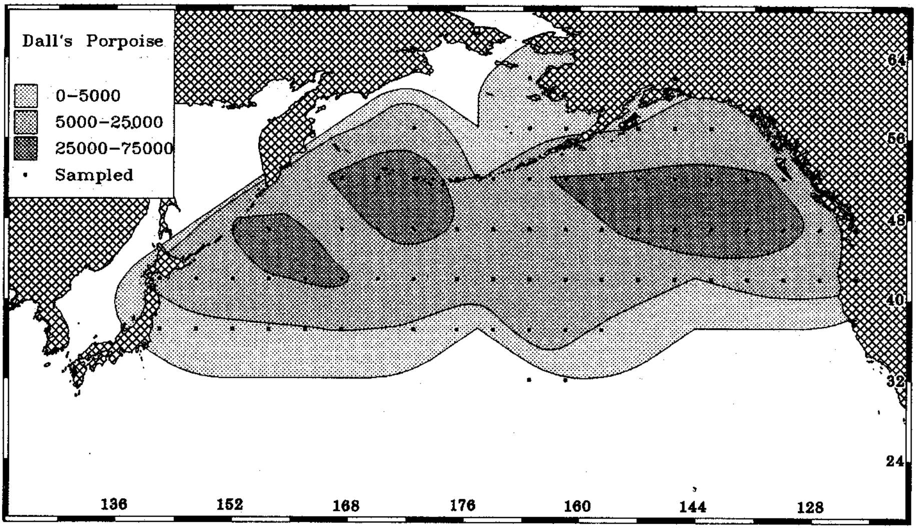

Fig. 13. Distribution of Dall's porpoises in the North Pacific. Dots indicate centers of 5° latitude × 5° longitude blocks for which data were compiled by Buckland et al. (1993); average densities indicated by contour isopleths are numbers of animals per 5° block.

the specific composition varying with location (Fiscus & Kajimura, 1981). Animals caught in the Japanese high seas salmon fishery in the North Pacific were consuming squid and 33 species of fishes, 94% of which were Myctophidae; of those, 78% were *Protomyctophum thompsoni* (Crawford, 1981).

Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) are also extremely abundant, with a population estimated to be 0.9×10^6 (Buckland et al., 1993). Their distribution is probably continuous across the N. Pacific, generally along the southern margin of the subarctic gyres, and extends southwards down the west coast of N. America to southern California. They may be somewhat more abundant in the WSA (Fig. 14), although the local concentrations depicted in these data may have been caused by seasonal movement patterns.

Northern right whale dolphins (*Lissodelphis borealis*) also are more abundant in the WSA along the southern margin (Fig. 15) with a population of about 0.07×10^6 (Buckland et al., 1993). Their distribution is probably more continuous than indicated by these data and the concentration shown near the coast of N. America probably represents a seasonal aggregation (R. Ferrero, pers. com.).

The habitat preferences of Dall's porpoises and Pacific white-sided dolphins are more similar than those of Northern right whale dolphins, a pattern apparently set by preferences for sea surface temperature (Ferrero, 1998). The zoogeographical ranges of Dall's porpoises and Pacific white-sided dolphins appear to be very similar, but they may still be selecting habitats on a finer scale than can be detected in existing data sets.

The diets of these two species of dolphins are similar, consisting of over 30 species of squids and fishes (Walker & Jones, 1993). Among northern right whale dolphins

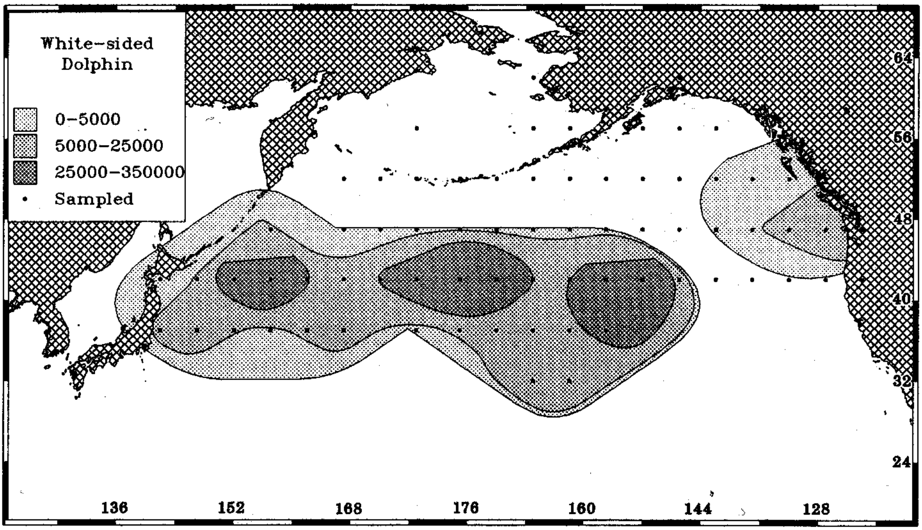

Fig. 14. Distribution of Pacific white-sided dolphins in the North Pacific. Dots indicate centers of 5° latitude × 5° longitude blocks for which data were compiled by Buckland et al. (1993); average densities indicated by contour isopleths are numbers of animals per 5° block.

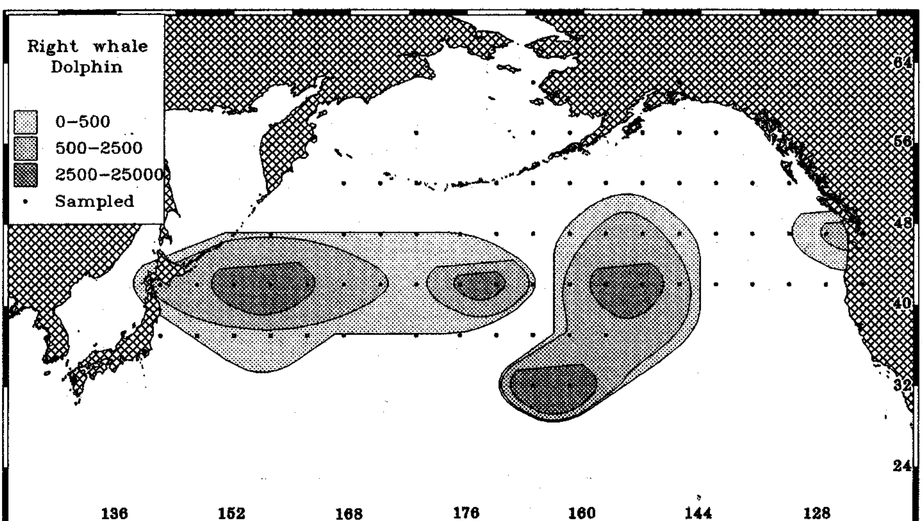

Fig. 15. Distribution of northern right whale dolphins in the North Pacific. Dots indicate centers of 5° latitude × 5° longitude blocks for which data were compiled by Buckland et al. (1993); average densities indicated by contour isopleths are numbers of animals per 5° block.

obtained in the squid fishery just south of the subarctic North Pacific in the Transision Domain, approximately 80% of the volume of prey was fishes and 20% was squid. Myctophids accounted for 68% of the fishes. Similarly, diets of Pacific white-sided dolphins were dominated by fishes, with Myctophidae accounting for 78% of the total. The most abundant squids in the diets, in decreasing order of importance, were *Abraliopsis felis*, *Onychoteuthis borealijaponica*, and several species of Gonatidae. Myctophids, particularly *Ceratoscopelus warmingi*, likewise dominated diets of common dolphins (*Delphinus delphis*) at about 40°N, 150°E in the western Transition Domain (Ohizumi, Yoshioka, Mori & Miyazaki, 1998).

Commercial whaling in the North Pacific from the 1950s through the 1970s caused severe population declines in fin whales (*Balaenoptera physalus*), sei whales (*B. borealis*), and sperm whales (*Physeter catodon*), as well as the remaining blue whales (*B. physalus*) and humpback whales (*Megaptera novaeangliae*) that had been heavily harvested in the first half of the century. By 1955 the oceanic waters off Kamchatka and the Commander Islands had lost their significance as whaling regions, whereas in the Sea of Okhotsk the stocks of whales had been exhausted even earlier. By 1975, the depletion of whales was apparent through the subarctic North Pacific.

Based on catch data compiled by the International Whaling Commission (IWC), fin whales concentrated on summer feeding grounds across the subarctic, with about equal densities in the WSA and ESA (Fig. 16). In summer, sei whales were concentrated generally south of the subarctic, and were more abundant across the WSA than in the ESA (Fig. 17).

Fin whales feed on zooplankton and a variety of species of small forage fishes, while sei whales are primarily planktivorous (Nemoto & Kasuya, 1965). The pre-

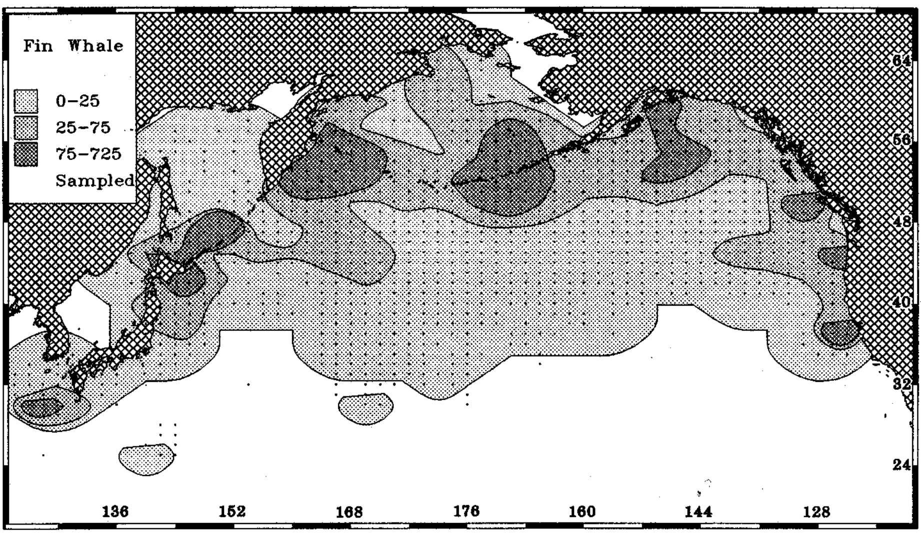

Fig. 16. Location of fin whales harvested in 1946 to 1975 in the North Pacific. Dots indicate centers of 5° latitude × 2.5° longitude blocks for which IWC data were compiled; average densities indicated by contour isopleths are numbers of animals harvested per block.

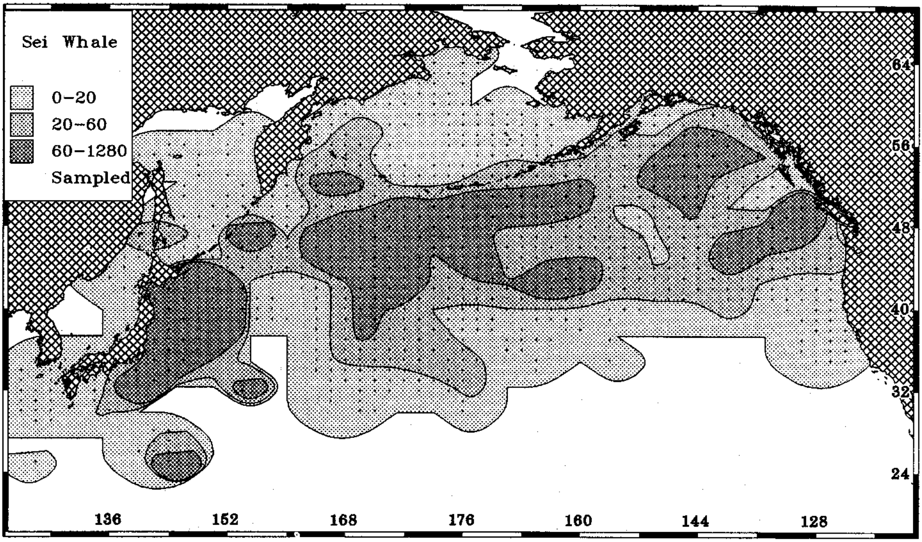

Fig. 17. Location of sei whales harvested in 1946 to 1975 in the North Pacific. Dots indicate centers of 5° latitude × 2.5° longitude blocks for which IWC data were compiled; average densities indicated by contour isopleths are numbers of animals harvested per block.

dominant zooplankton prey of both species are euphausiids, principally *Thysanoessa* spp., and the copepods *Neocalanus cristatus* and *N. plumchrus*. The overall distribution of fin and sei whales in summer in the subarctic North Pacific coincided closely with the distribution of zooplankton biomass (Sugimoto & Tadokoro, 1997).

The smaller minke whales (*Balaenoptera acutorostrata*) are common throughout the North Pacific (Jefferson, Leatherwood & Webber, 1993), although they are not abundant—in the WSA there are about 6000 individuals (Buckland & Cattanach, 1992). They are comparatively concentrated, however, off the coast of Hokkaido and near the center of the WSAG (Kasamatsu & Hata, 1985). Minke whales randomly sampled from the WSA in the summers of 1994 and 1995 were consuming a variety of fishes and crustaceans (Tamura, Fujise & Shimazaki, 1998). Their diets were dominated by Pacific saury (77% frequency of occurrence and 81% of biomass), but intermittently Japanese anchovy (*Engraulis japonicus*), Japanese pilchard (*Sardinops melanostictus*), and euphausiids were important.

The subarctic is the home to most of the North Pacific population of sperm whales during much of the year, particularly summer (Fig. 18). Males and females of the northeastern stock were abundant in summer in the ESA, but females were uncommon in the western portion. Kasuya and Miyashita (1988) interpret this as a consequence of females avoiding the intrusion of relatively cold water, rather than as being an artifact of seasonal sampling. Males of the northwestern stock moved into the Bering Sea in summer, while females were found around the perimeter of the WSA. Females were uncommon in the center and western part of the WSA, however, which was interpreted in the same way as in the ESA, a consequence of the intrusion of

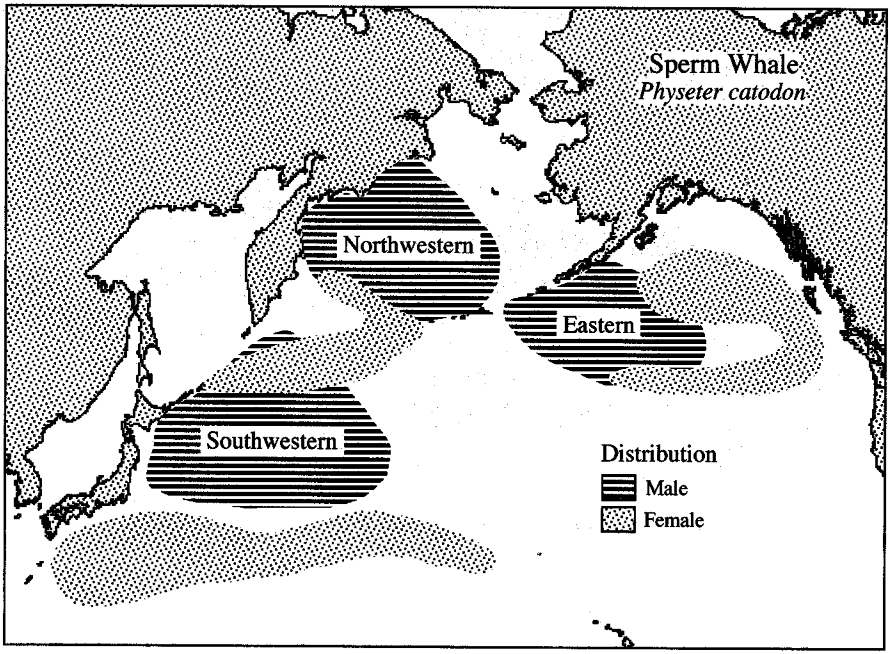

Fig. 18. Distribution of sperm whale stocks in the North Pacific as described by Kasuya and Miyashita (1988).

cold water. Some males of the southwestern stock were found in the southwestern portion of the WSA.

Harvest data of the IWC, however, show a different picture of sperm whale distribution in the North Pacific, at least for the summer season when the whales were on their feeding grounds. Females concentrated mainly south of the Subarctic Boundary in the western part of the North Pacific Current (Fig. 19). Comparatively small numbers occurred farther north, most of which were off the west coast of North America at about the latitude of the Transition Domain. In the subarctic, female sperm whales were more abundant in the WSA than in the ESA. Likewise, male sperm whales also were more abundant in the WSA than in the ESA (Fig. 20).

Throughout their range, sperm whales eat both squid and fish, although squids are likely to be the principal prey overall. In the early 1960s in the North Pacific, squids were predominant in diets of sperm whales from the Aleutian Islands, and were of similar importance to fish in the diets of sperm whales taken along the shelf edge of the Gulf of Alaska (Okutani & Nemoto, 1964). Squids comprised 95% of the biomass of prey in diets of sperm whales taken near the Kurile Islands, and three species (*Gonatus magister*, *G. fabricii* and *G. simile*) accounted for 60% of the total. Likewise, near the Commander Islands, 74% of the stomachs of sperm whales examined contained only squid, while 24% contained squid and fish, and 1.4% contained only fish.

The beaked whales (Ziphiidae) are the least known of all whales in the North

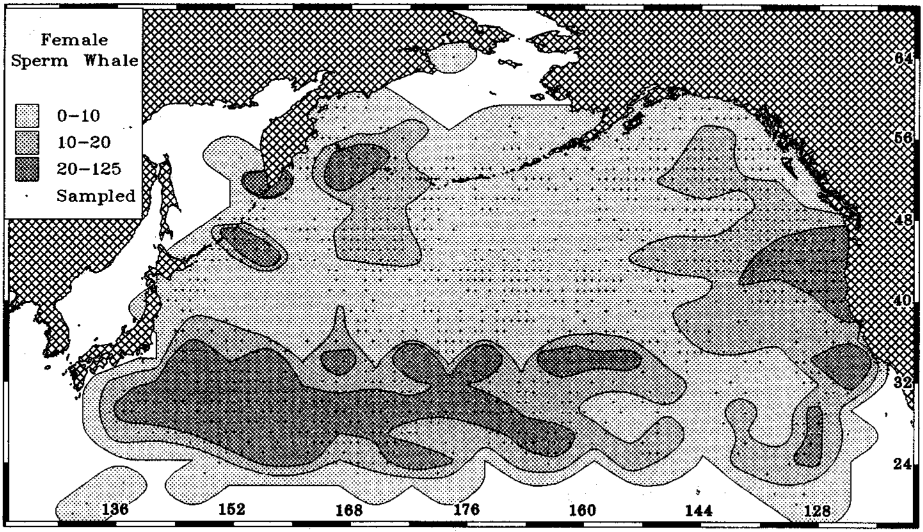

Fig. 19. Location of female sperm whales harvested in 1946 to 1979 in the North Pacific. Dots indicate centers of 1° latitude × 1° longitude blocks for which data were compiled by the IWC; average densities indicated by contour isopleths are numbers of animals harvested per 1° block.

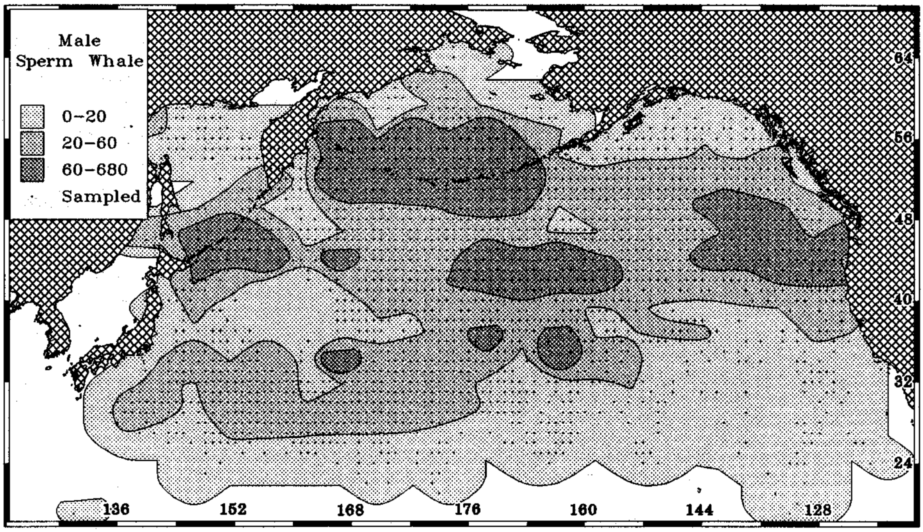

Fig. 20. Location of male sperm whales harvested in 1946 to 1979 in the North Pacific. Dots indicate centers of 1° latitude × 1° longitude blocks for which data were compiled by the IWC; average densities indicated by contour isopleths are numbers of animals harvested per 1° block.

Pacific. However, when Baird's beaked whale (*Berardius bairdii*) became the target of Japanese whaling in the western North Pacific, an effort was made to define their distribution (Fig. 21). Based on the combined observations from Japanese whale scouting boats in March through October between 1964 and 1982, Baird's beaked whales were commonly found in the WSA off the coast of the Kamchatka Peninsula and in an arc extending between there, the central North Pacific, and the west coast of North America. Very few were seen in the ESA.

Diets of beaked whales are predominantly cephalopods, especially squids (Lowry, Frost, Calkins, Swartzman & Hills, 1982).

4.2. Pinnipeds

The most abundant of the pinnipeds found breeding and hauling-out around the perimeter of the subarctic North Pacific has been the Steller sea lion. However, in the last 25 years the abundance of sea lions has declined by some 80% across most of its range; the principal exception being in the eastern North Pacific from southeastern Alaska through British Columbia (Loughlin, Perlov & Vladimirov, 1992; NMML, 1994; NMML unpubl. data). Formerly, its numerical distribution approximated that shown in Fig. 22 with its highest density occurring in the Aleutian Islands and western Gulf of Alaska, and lower densities occurring in the western and eastern North Pacific.

Most sea lions stay near rookeries in summer, generally foraging over the continental shelf, although occasionally they venture off the shelf to forage in deep water (Kajimura & Loughlin, 1988; Merrick & Loughlin, 1997). The diets of the sea lions

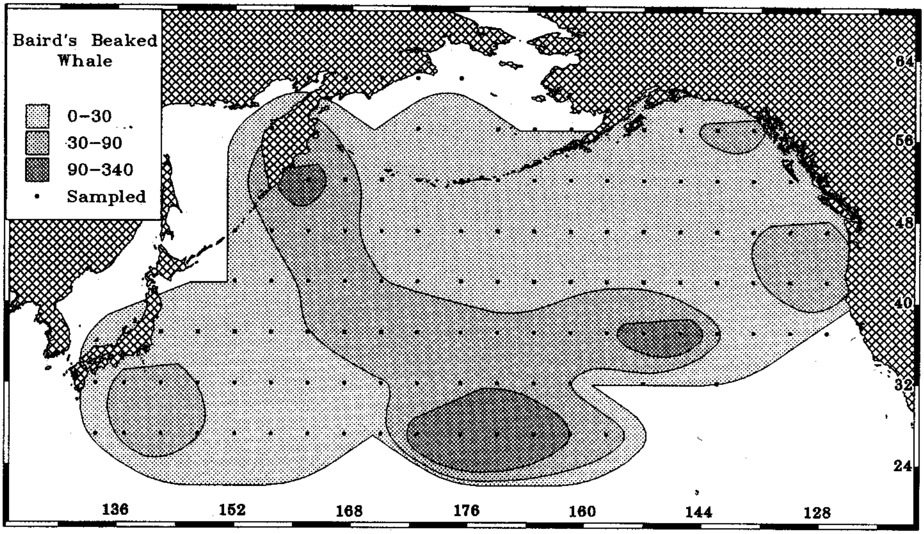

Fig. 21. Distribution of Baird's beaked whales in the North Pacific. Dots indicate centers of 5° latitude × 5° longitude blocks for which data were compiled by Kasuya and Ohsumi (1984); average densities indicated by contour isopleths are numbers of animals per 5° block.

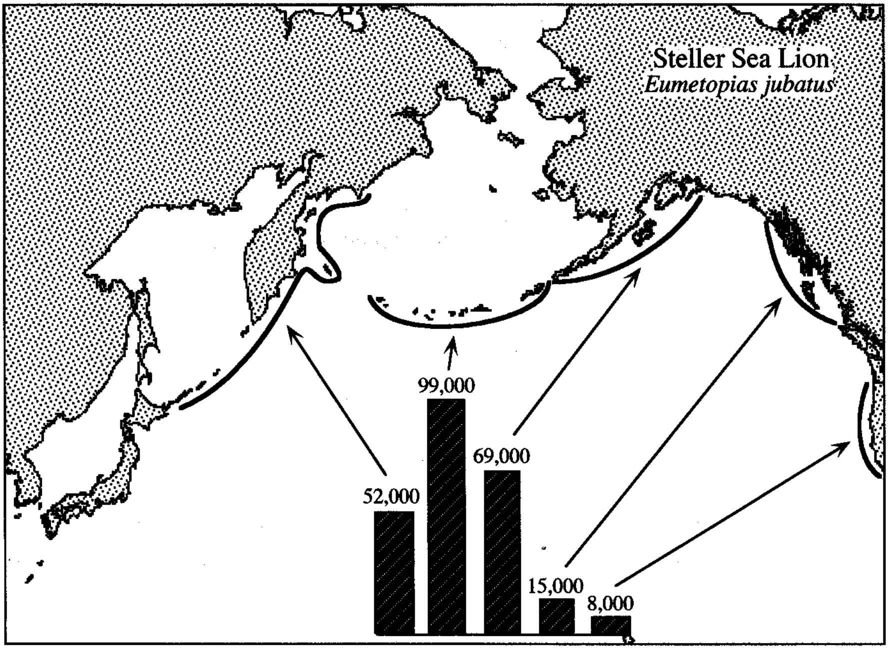

Fig. 22. Estimated historical abundance of Steller sea lions in regions of the North Pacific. From data in Loughlin et al. (1992).

consist primarily of fishes common to shelf and shelf-edge areas, including walleye pollock, Atka mackerel, salmon (*Onchorynchus* spp.), flatfishes (Pleuronectidae), and various species of smaller forage fishes such as herring (*Clupea harengus*), capelin, and sand lance (Mathisen, Baade & Lopp, 1962; Merrick & Calkins, 1996; Pitcher, 1981; Thorsteinson & Lensink, 1962). There is considerable regional and seasonal variability in diets.

Northern fur seals are more abundant than sea lions by approximately an order of magnitude, but the major rookery (> 70% of the total population) is on St. Paul Island (Pribilof Islands) in the Bering Sea (Lander & Kajimura, 1982). Outside the breeding season, fur seals are highly pelagic. Most animals from the Pribilof Islands winter along the west coast of North America south to California, whereas those from rookeries in the Commander Islands and Sea of Okhotsk winter off the coast of northern Japan. A substantial number are to be found across a broad area of the North Pacific throughout the year (NMFS, 1993; Fig. 23). Buckland et al. (1993) estimated approximately 175 000 in the open North Pacific south of the Aleutian Islands to 25°N and across the breadth of the ocean from Japan to North America.

The majority of animals at sea in the open N. Pacific are probably juvenile males from the Pribilof Islands. Males tracked from the Pribilofs exhibited two distinct migration patterns in fall and winter (Fig. 24). One pattern was of animals moving into the central portion of ESA and the other was of animals moving into the southern portion of the WSA. In the ESA, fur seals appeared to move along the northern

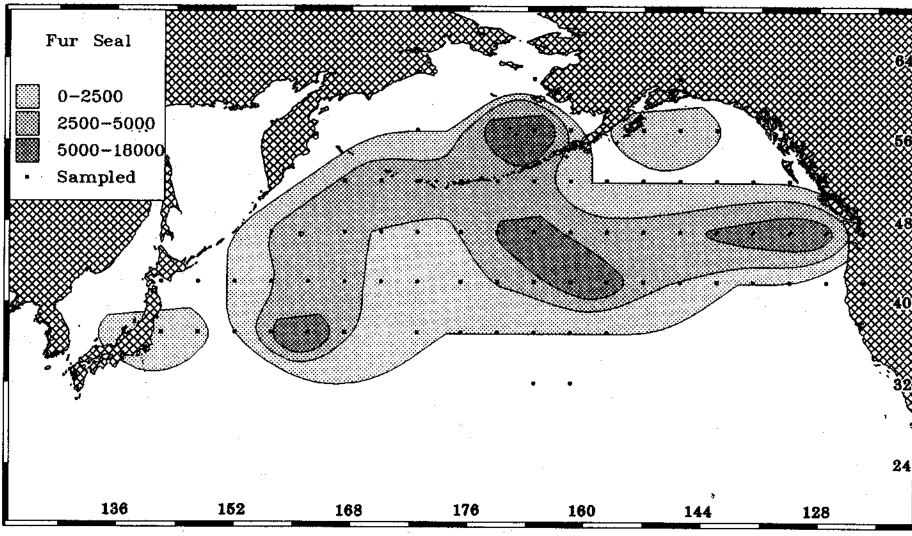

Fig. 23. Distribution of northern fur seals in the North Pacific. Dots indicate centers of 5° latitude × 5° longitude blocks for which data were compiled by Buckland et al. (1993); average densities indicated by contour isopleths are numbers of animals per 5° block.

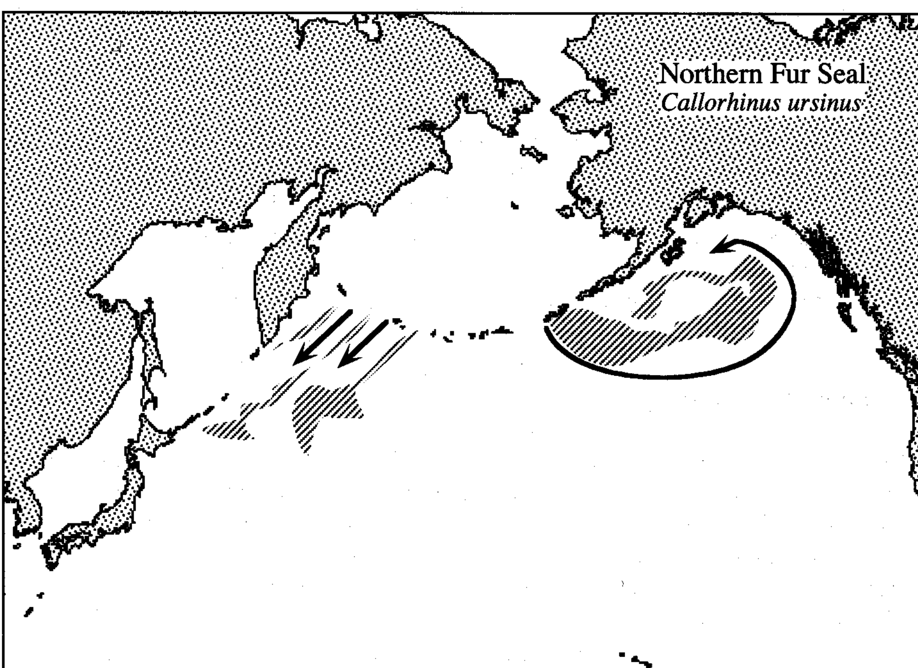

Fig. 24. Areas enclosing movements of male northern fur seal from the Pribilof Islands in fall–winter (hatching): arrows indicate direction of movements. Redrawn from Loughlin et al. (1999).

margin of the Subarctic Current and into the gyre. Loughlin, Ingraham, Baba and Robson (1999) suggest that seals favor the perimeter of the gyre because of elevated prey abundance.

Fur seals from the ESA in spring (April–June) have diets consisting primarily of gonatid squids, with most of the balance being made up of salmon and rockfishes (Scorpaenidae) (Perez & Bigg, 1986). Information from animals taken in the North Pacific squid drift net fishery indicate that Myctophidae and squids constitute the bulk of the diet (Walker & Jones, 1993).

The ESA is also important to northern elephant seals. Males spend about 250 days y^{-1} and females about 300 days y^{-1} there (Stewart & DeLong, 1995). Both sexes return to island rookeries in California for two short periods for the breeding season and later again to molt. Males mostly inhabit the northern perimeter of the eastern gyre just off the edge of the continental shelf during both the postbreeding and postmolt periods (Fig. 25). Females tend to occupy the southeastern edge of the gyre during the postmolt period but move somewhat farther north and west in the postbreeding period.

The specific composition of the diets of elephant seals while in the ESA is unknown, although information does exist on diets from the west coast of North America between Mexico and Oregon, especially from rookeries on San Miguel Island and Ano Neuvo Island (Antonelis, Lowry, DeMaster & Fiscus, 1987; Condit & Le Boeuf, 1984). There, the diets consisted of a variety of teleost and cartilaginous fishes and invertebrates. Squids were the dominant prey, but the pelagic red crab (*Pleuroncodes planipes*) and Pacific whiting (*Merluccius productus*) were also common. At sea in the ESA, elephant seals dive constantly to depths of 250–550 m (Stewart & DeLong, 1995). A prominent layer of biomass occurs in the ESA at about 300–400 m in depth, and a portion of this layer migrates to near the surface at night (Frost & McCrone, 1979). Species in this layer are predominantly myctophids, especially *Stenobrachius leucopsarus*, euphausiids, especially *Euphausia pacifica*, and the penaeid decapod shrimp *Sergestes similis*. All of these species are potential prey of elephant seals. The abundant squids in the ESA that are consumed by numerous other predators are undoubtedly targeted by the seals as well.

5. Temporal variability

Very little is known about levels of interannual or longer-term variability in any aspect of the ecology of marine birds or mammals at sea in the subarctic North Pacific. Around the margin inshore, the collapse of the sea lion population is perhaps the greatest regional signal, but beyond a general belief that inadequate prey resources have been in some way responsible, the cause of this decline has yet to be firmly established (Anonymous, 1993).

The reliance of sea lions on shelf prey species complicates an assessment of relationships between gyres and the population dynamics of these animals. However, the decline in most of the range coincided with the meteorological regime shift of the mid-1970s that had numerous other biological correlates over a broad area of

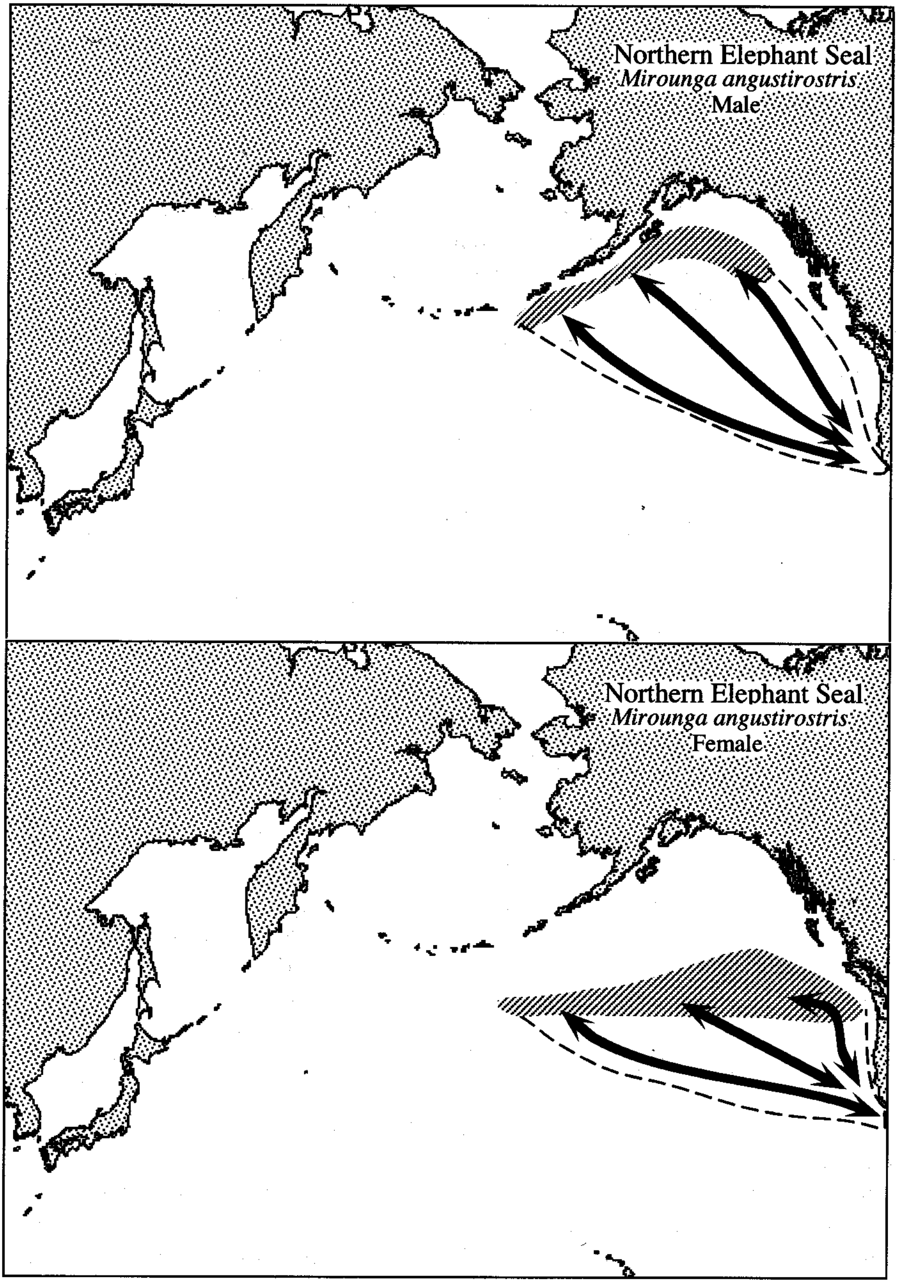

Fig. 25. Generalized migration routes and endpoints of northern elephant seals in the North Pacific. Hatching shows migration end points; bold arrows show migration routes; dashed lines enclose migration corridors. Redrawn from Stewart and DeLong (1995).

the North Pacific (Brodeur, Frost, Hare, Francis & Ingraham, 1996; Ebbesmeyer, Cayan, McLain, Peterson & Redmond, 1991; Francis & Hare, 1994; Mantua, Hare, Zhang, Wallace & Francis, 1997; Springer, 1998). Amongst these was a dramatic decline in abundance of harbor seals (*Phoca vitulina*) in the Gulf of Alaska (Pitcher, 1990) and a decline in growth rates of fur seals from the Pribilof Islands (A. Trites, unpubl. data). Data on fur seals from the Pribilofs are relevant because the animals achieve their annual growth increment as they migrate northward in spring through the ESA (Trites & Bigg, 1996). Thus, conditions in the greater subarctic North Pacific appear to be connected to the health of populations of pinnipeds inhabiting the margins or migrating through the region.

Likewise, several species of seabirds nesting in the Gulf of Alaska experienced a decrease in breeding success and abundance in the mid-1970s that coincided with shifts in diet, indicating changes in prey populations (Piatt & Anderson, 1996). Like sea lions and harbor seals, the seabirds that nest around the edge of the ESA forage over the shelf during summer and rely on the common prey species in that habitat (DeGange & Sanger, 1986; Piatt & Anderson, 1996). How variability in the gyres might have caused or contributed to these changes is difficult to assess. Some species, such as tufted and horned puffins overwinter in the subarctic gyres and it is a nursery area for juveniles. Several other species, like the black-legged kittiwake, range widely over the North Pacific and are common in the ESAG in winter. Thus, winter food supply and the resulting body condition of birds entering the breeding season lay the foundation for subsequent breeding success. Furthermore, forage fish production over the shelf and in coastal areas may be profoundly influenced by conditions in the subarctic North Pacific. Variability in total zooplankton production, or the timing of the zooplankton maximum biomass, in the ESA appears to affect recruitment and production of forage fishes, groundfishes, and salmon in continental shelf areas of the northeast Pacific (P. Anderson and J. Piatt, pers. comm.).

During the 1990s, there were significant changes in the ecosystem of the WSA which are believed to have been generated by decadal-scale fluctuations in the global climate and oceanographic regimes (Shuntov, Dulepova, Radchenko & Lapko, 1996). The most profound transformation occurred in fish populations around the Kurile Islands (Table 6) with the dramatic decline of populations of sardines (*Sardinops sagax*) being of particular importance for piscivorous birds. This decline was only partially offset by increases in numbers of other fishes and squids (Ivanov, 1997). This change has not yet reversed and the populations are still in the process of reorganization.

Similarly, in the ESA there were large differences in the relative abundances of fishes and squids in the 1980s compared to the 1950s, with some species increasing greatly and others declining greatly between these two periods (Table 7). Such adjustments in patterns of production in the pelagic system can be expected to have had coupled effects on the higher trophic levels.

In extreme cases of El Niño events, conditions in the ESA deteriorate to the point that inshore and pelagic seabirds suffer pronounced food shortages and starvation. In 1983, 1993, and 1997 mass mortalities of several species of seabirds occurred

Table 6
Biomass and relative abundance of principal fishes and squids in epipelagic waters (< 200 m) in the N. Pacific Ocean off the Kurile Islands in the 1980s and 1990s. Values in tonnes (% of total)[a]

English Name	Scientific Name	1980s	1990s
Pacific sardine	*Sardinops sagax*	2000 (49)	200 (8.9)
Walleye pollock	*Theragra chalcogramma*	850 (21)	200 (8.9)
Salmon	*Salmonidae*	200 (4.9)	300 (13)
Lanternfish	*Myctophidae*	400 (9.8)	450 (20)
Pacific saury	*Cololabis saira*	400 (9.8)	600 (27)
Japanese anchovy	*Engraulis japonicus*	50 (1.2)	200 (8.9)
Other fishes		100 (2.4)	100 (4.4)
Squids		100 (2.4)	200 (8.9)
Total		4100 (100)	2250 (100)
t km^{-2}		7.2	4.0

[a]From Shuntov et al. (1996).

Table 7
Biomass and relative abundance of principal fishes and squids in epipelagic waters of the eastern subarctic Pacific in the 1950s and 1980s. Values in no km^{-1} 12 h^{-1} (% of total)[a]

English Name	Scientific Name	1950s	1980s
Steelhead	*Oncorhynchus nerka*	0.35 (1.8)	0.56 (1.1)
Salmon shark	*Lamna ditropis*	1.4 (6.9)	1.7 (3.5)
Blue shark	*Prionace glauca*	0.20 (1)	0.28 (0.6)
Jack mackerel	*Trachurus symmetricus*	4.0 (20)	0.70 (1.5)
Pacific pomfret	*Brama japonica*	12 (59)	21 (43)
Albacore	*Thunnus alalunga*	0.16 (0.8)	0.42 (0.9)
Neon flying squid	*Ommastrephes bartrami*	1.8 (9.2)	22 (45)
Nail squid	*Onychoteuthis borealijaponicus*	0.10 (0.5)	0.59 (1.2)
Eight arm squid	*Gonatopsis borealis*	0.26 (1.3)	1.5 (3)
Total		20.27	48.75

[a]From Brodeur and Ware (1995).

around the margin of the ESA, as well as north into the Bering and Chukchi seas (Mendenhall, 1997; Nysewander & Trapp, 1984; Piatt & van Pelt, 1993).

6. Discussion

The area of the region encompassing the subarctic gyres of the North Pacific Ocean is small by comparison to the total area of the North Pacific, but it is immense compared to what is visible to observers censusing seabirds and marine mammals from the decks of ships en passage. Thus, great care must be taken when interpreting such census data to characterize the importance of the gyres to marine birds and mammals, and especially when making comparisons between east and west. The data are generally sparse and so we caution that the characterizations and comparisons made both previously and herein should be considered tentative.

An additional complication of assessing the relative importance of gyres is that they are not spatially homogeneous with respect to physical and biological features of relevance to birds and mammals. For example, in the western subarctic in the vicinity of the Kamchatka Peninsula and Commander Islands, areas of continental shelf and slope support abundant macroplankton with biomasses of about 150 t km^2 (VPS). Further offshore in the areas extending up to 200 km from the coast, the concentrations decrease by a factor of 2–2.5, whereas near the Kurile Islands the concentrations and biomass of macroplankton remain almost unchanged at 150–250 t km^{-2} up to 100–200 km off the coast. The same pattern has been observed in the distribution of nekton, excluding cephalopods: in the vicinity of the Kamchatka Peninsula and Commander Islands, areas of the continental shelf and slope have a higher biomass than in the open ocean, whereas near the Kurile Islands concentrations are higher and distribution is more even.

The need to consider spatial scales such as these constrains the sample size of observations available to describe distributions of birds and mammals and their trophic relationships. Similarly, interannual and long-term variability in marine production and the need for sampling intervals comparable in time across spatial domains further dilutes sample sizes appropriate for descriptive and comparative purposes.

In contrast, the distribution and abundance of marine birds and mammals breeding on the coasts around the perimeter of the subarctic gyres is comparatively well known. Spatial comparisons can be made with some confidence, although it remains to be shown whether regional differences are functions of the environmental quality of the gyres as foraging habitat, the availability and suitability of terrestrial habitat for nesting, rookery, and haul out sites or the evolutionary and recent distributional history of the various species inhabiting the North Pacific.

6.1. Distributions

All of the most abundant species of resident North Pacific seabirds are more numerous in summer in the WSA than in the ESA. The numbers of visiting migrant southern hemisphere shearwaters are 3–4 times greater in the WSA and the number of Laysan albatrosses from the central Pacific is nearly two orders of magnitude greater. Only one of the 14 common species, the black-footed albatross, is more abundant in the ESA than in the WSA. Thus, if the densities of those pelagic seabirds which are not constrained in their distribution by requirements imposed by nesting are higher in WSA, this would support the idea that secondary production and/or foraging opportunities are consistently better in the WSA than in the ESA.

Amongst the marine mammals for which there are good distributional data, the sei whale was more abundant in the WSA, as are at present white-sided dolphins and right whale dolphins. However, the latter two species are distributed generally south of the subarctic. Fin whales were uniformly distributed across the breadth of the subarctic North Pacific. Dall's porpoises are perhaps more abundant in the ESA.

Male sperm whales were more abundant in the WSA, but these whales were likely to have been exploiting foraging opportunities created by processes specific to the Aleutian Islands and so their distributions were probably not indicative of conditions in the WSA compared to the ESA.

The relative abundance of fur seals at sea in the subarctic North Pacific is influenced by the migration routes the animals take between their rookeries and their wintering areas far to the south. The observations reported by Buckland et al. (1993) indicate the route south from the Pribilof Islands crosses the western portion of the ESA and then passes east around its southern margin towards the coast of the Pacific Northwest. The distribution of fur seals around the periphery of the ESA is supported by the data of Loughlin et al. (1999). Fur seal distribution in the ESA is similar to that of seabirds in that they both tend to avoid the center of the gyre.

6.2. *Environmental correlates of distributions*

The surface nitrate distribution in the North Pacific indicates that the area of influence of the WSAG is larger than that of the ESAG (NODC, 1998). This broader areal extent, together with the higher concentrations of nitrate in the central region of the WSAG, suggest that circulation is more intense with greater Ekman pumping and higher production potential there than in ESAG. This, coupled with the more complex oceanography in the WSA, is consistent with there being greater zooplankton biomass in the WSA than in the ESA (Sugimoto & Tadokoro, 1997).

The complex and powerful hydrodynamics in the region of the Kurile Islands, from the confluence of the Kuroshio and Oyashio currents and along the Kamchatka Peninsula are additional important features of the physical regime of the northwestern Pacific that contribute to a high biomass of plankton and nekton. Strong upwelling currents near the islands, as well as numerous frontal zones and eddies supply macronutrients and promote plankton growth throughout summer (Lapshina, 1996). Entrainment of plankton at fronts, such as those associated with eddies, can enhance transfer of biomass between trophic levels. Higher production at the base of the food web in the WSA is consistent with the observations of a greater biomass of seabirds and baleen whales in summer in the WSA.

In the ESA, zooplankton biomass in spring and summer appears to be higher around the margins than in the center (Brodeur & Ware, 1992; Parsons & LeBrasseur, 1968), and the growth rates of the copepods *Neocalanus plumchrus* and *N. flemingeri* are faster around the margins than in the centers (Miller et al., 1988). According to the model of Parsons and LeBrasseur (1968), the distribution of zooplankton biomass in time and space corresponds to temporal and spatial patterns of primary production, which might further explain differences observed in growth rates between the center and the edge. Furthermore, Ekman pumping would tend to transport biomass away from the center of the gyre towards the perimeter as described by Cooney (1986) when accounting for the seasonal presence of zooplankton over the shelf of the northern Gulf of Alaska. These processes appear to be reflected in the distributions of seabirds, fur seals, and elephant seals, which are likewise more abundant around the perimeter of the eastern gyre.

6.3. Trophic dependencies

A large number of species of fish and invertebrates are consumed by seabirds and marine mammals in the North Pacific. All have some trophic importance as a result of the opportunistic feeding stategies of generalist predators in pelagic ecosystems. However, the number of species that make a substantial contribution to the biomass consumed is small compared to the total inventory of species present. Myctophids and squids are of greatest overall importance over the deep water off the continental shelf in the WSAG. Atka mackerel, three-spined stickelbacks, and lancetfish are consumed by several species. Of these, the Atka mackerel is of greatest importance. It is consumed regularly by thick-billed murres, tufted puffins, short-tailed shearwaters, and sea lions, and occasionally by horned puffins, crested auklets, which are normally planktivorous, ancient murrelets (*Synthliboramphus antiquus*), and Arctic loons (*Gavia arctica*) in the subarctic North Pacific (Ogi, 1980).

Pacific saury is of particular importance to sooty shearwaters and minke whales in the WSA, although it is not abundant in diets of other species of seabirds or marine mammals there. The prevalence of sauries in the diets of sooty shearwaters in the WSA and their absence in diets of the other species of seabirds, at least, is likely related to the seasons and locations at which the birds were collected and the seasonal movements of sauries. The short-tailed shearwaters, murres, and puffins Ogi (1980) examined were mainly taken in spring from waters to the north of the Transition Domain, while the Sooty Shearwaters were mostly taken in summer from the Subarctic Current and Transition Domain (i.e. somewhat farther south and later in the season). If samples of the other species had been collected later in summer, saury might have been of more importance. Ogi (1980) reported that saury were being consumed by thick-billed murres in April just south of the Subarctic Boundary, indicating that saury is acceptable prey for murres. Saury is important in diets of Buller's and flesh-footed shearwaters in the Transition Domain, and could be expected to become more important for other seabirds as summer progresses and the fish migrate into more northerly waters.

The importance of jellyfish in diets of seabirds is probably underestimated in most studies because they are rapidly and completely digested. They are eaten by a large variety of seabirds (Harrison, 1984), including fulmars, short-tailed shearwaters, and sooty shearwaters in the subarctic N. Pacific, as noted above. Jellyfish are also eaten by Laysan albatrosses and flesh-footed shearwaters and stable isotope ratios of these birds, and of Buller's shearwater, from the Transition Domain suggest that jellyfish consumption could be considerably greater than indicated by the analysis of stomach contents (Gould et al., 1997a, 1997b, 1998).

The majority of data of diets of marine birds and mammals in the North Pacific has come from the WSA and Transition Domain. Data from offshore in the ESA are fewer, but in the case of toothed cetaceans, at least, indicate that squids are the dominant prey there as well (Kajimura & Loughlin, 1988). Although taxonomic comparisons between subarctic regions cannot be made at present, it seems likely that prey in the ESA are the same as in the WSA.

7. Conclusions

Seabird biomass in the subarctic North Pacific Ocean is concentrated over the shelf and slope near the continents in all seasons. Densities at sea in the open ocean are small by comparison. Seabird densities are higher in the WSA than in the ESA, and the contrast is particularly noticeable in the centers of the gyres. Known prey of the seabirds consists primarily of squids, Myctophidae, *Pleurogrammus* spp., sticklebacks, and smooth tongue. Pacific saury is important in parts of both gyres, particularly in summer when the fish move north.

The most abundant cetaceans in the northern North Pacific are Dall's porpoise and sperm whales. Dall's porpoises appear to be evenly distributed across the ESA and WSA. Sperm whales may be more abundant in the WSA than in the ESA because two stocks of whales utilize the WSA. In summer male sperm whales are associated more with the Aleutian Islands where there are local production processes which are not strictly associated with features of the gyres. Fin whales and sei whales, which were formerly numerous, were both apparently more abundant in the WSA than in the ESA.

Only two species of pinnipeds, the northern fur seal and northern elephant seal, use the open ocean regions of the gyres to any extent; the numerous other species occurring in the North Pacific seldom venture far from shelf waters.

Squids and Myctophidae dominate the diets of Dall's porpoises, dolphins, sperm whales, and fur seals. Pacific saury are important to minke whales. Zooplankton are preyed on by fin and sei whales. The diets of elephant seals are not known, but are likely to be dominated by squids.

The more complex physical oceanographic environment and more intense circulation in the WSA probably account for its higher primary and secondary production. Marine birds and mammals are distributed more evenly across the whole region of the WSA gyre, whereas in the ESA, abundance of several species appears to be greatly reduced in the centre, compared with the richness of the Subarctic Current and Alaska Stream around its periphery. Such a distribution is probably the result of physical processes and patterns of food web development that lead to higher abundances of prey at the margins.

Decadal-scale variability in physical conditions and biological production, around the margin of the WSA and ESA, has led to major fluctuations in the abundance, productivity, and growth of several species of marine birds and mammals in the North Pacific. Seabirds in the subarctic are also susceptible to effects of extreme interannual variability, such as are visited upon the region by El Niño events.

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